THE UNIVERSITY OF ALBERTA

HABITAT SELECTION AND RESOURCE DIVISION AMONG BIGHORN SHEEP, ELK AND MULE DEER IN WESTERN ALBERTA

by

© LUIGI E. MORGANTINI

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(Signed) Luigi E. Morgantini

PERMANENT ADDRESS:

Luigi E. Morgantini
34, 11110-68 Ave.
Edmonton, Alta. T6H 2C2

DATED April 17 1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Habitat selection and resource division among bighorn sheep, elk and mule deer in western Alberta" submitted by Luigi E. Morgantini in partial fulfilment of the requirements for the degree of Master of Science in Wildlife Productivity and Management

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Supervisor

J. Thompson
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....
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DATE......April 17/1979.......

ABSTRACT

A study on habitat selection and resource division among bighorn sheep, elk and mule deer was conducted on the Ya Ha Tinda Ranch in western Alberta during the winter and spring of 1975-76.

The vegetation of the study area was classified into eighteen types based primarily on their structure. The distribution of animals was determined from direct observation. Meteorological conditions, site descriptors and other biotic and abiotic factors were recorded and regarded as potential determinants of animal distribution.

Analysis of 470 group sightings (24,612 individuals) indicated a discrete pattern of habitat selection. Bighorn sheep were found largely associated with open mountain ranges but occurred at lower elevation in spring. A sex differential in habitat use and spatial distribution between rams and ewes was observed. Elk were observed mostly on the valley floor, on the open grasslands and in the surrounding forests. However, their distribution and activity patterns appeared to be affected by human disturbance. Mule deer, present in the study area during spring months, made use of several coniferous and deciduous forest types and generally occurred in habitats of high heterogeneity.

Although no behavioral response to cold weather was recorded, bighorn sheep and mule deer sought shelter in spring during warm, clear days.

A definite pattern of resource partitioning among bighorn sheep, elk and mule deer was found. In winter, elk and bighorn sheep used different vegetation types and were observed in diverse physical environments. Bighorn sheep were found at high elevation and on steep and rugged country, whereas elk preferred lower elevation and less steep, grassy ranges. In spring, bighorn sheep and elk continued to be distinct in their use of vegetation types, but mule deer overlapped to a certain degree with both species. However, the three ungulate species were separated on the basis of the degree of habitat heterogeneity and in their distribution in the physical environment. Mule deer were observed generally at an elevation intermediate between bighorn sheep and elk. Ecological separation was achieved on a combination of vegetational and physiographic parameters and was reflected by a species-specific spatial distribution. The marginal spatial overlap between the species was considered insignificant with populations at the present levels.

This study indicated several factors which may alter resource partitioning. Among these the behavioral response of elk to human disturbance appeared most important. Harassment in winter during a special hunting season displaced elk from their prime winter range on the main grassland and forced them to overlap with bighorn sheep. The thermal environment also was found to affect resource partitioning. Use of deciduous forests by bighorn sheep, for instance, and their consequent overlap with mule deer in

spring was interpreted largely as a response to warm weather.

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This study was conducted under the supervision of Dr. R.J. Hudson whose guidance proved extremely valuable and instrumental for the completion of the project. I am particularly grateful to him for his patience, trust and moral support showed when I delayed the writing of this thesis because I was involved in another study. My special thanks are also extended to the members of my committee, Dr. J.F. Addicot, Dr. J.R. Thompson and Mr. W.D. Wishart.

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ABOUT THE PRINCIPLE OF COMPETITIVE INTERACTIONS:

"...the concept is in itself misleading. It has fostered pointless controversy about the possibility of coexistence of competitors, when what is needed is explanation of the fact that they do coexist".

Darlington, 1972

INTRODUCTION

The importance of studies at a community level has been recognized by ecologists for many years (Elton and Miller, 1954). However, among numerous studies dealing with food habits, habitat selection and behavior of different ungulates, few have been concerned with mixed-grazing systems.

In the Ya Ha Tinda Ranch, where most of this study was conducted, large numbers of elk (Cervus elaphus nelsoni), bighorn sheep (Ovis canadensis canadensis), and mule deer (Odocoileus hemionus hemionus) occur in the same restricted area. The use of the ranch as pasture for horses in winter and spring, increasing recreational use and new pressures for resource development make the management of that wildlife community difficult. The present study stemmed from the need for a better understanding of the ecology and behavior of the wildlife species in the area.

The objective was to determine the manner in which ungulate species in a mixed assemblage co-exist by division of habitat resources. An attempt was made to define the operational components which had an effect on the animal and caused some response, either physiological or behavioral. The approach involved the following:

1. Identification and representation of important resource vectors along which ecological separation was

achieved.

2. Identification of factors which may alter the pattern of use of each of these resource dimensions and hence alter functional inter-relationships.

This thesis is structured in five chapters. The first chapter presents features of the area where field work was conducted. In the second chapter major vegetation types are identified. The third chapter describes occupational patterns and spatial distribution of each species. Partitioning of the identified resources is then discussed in the fourth chapter. Finally, the last chapter highlights conclusions and management considerations.

CHAPTER ONE

STUDY AREA

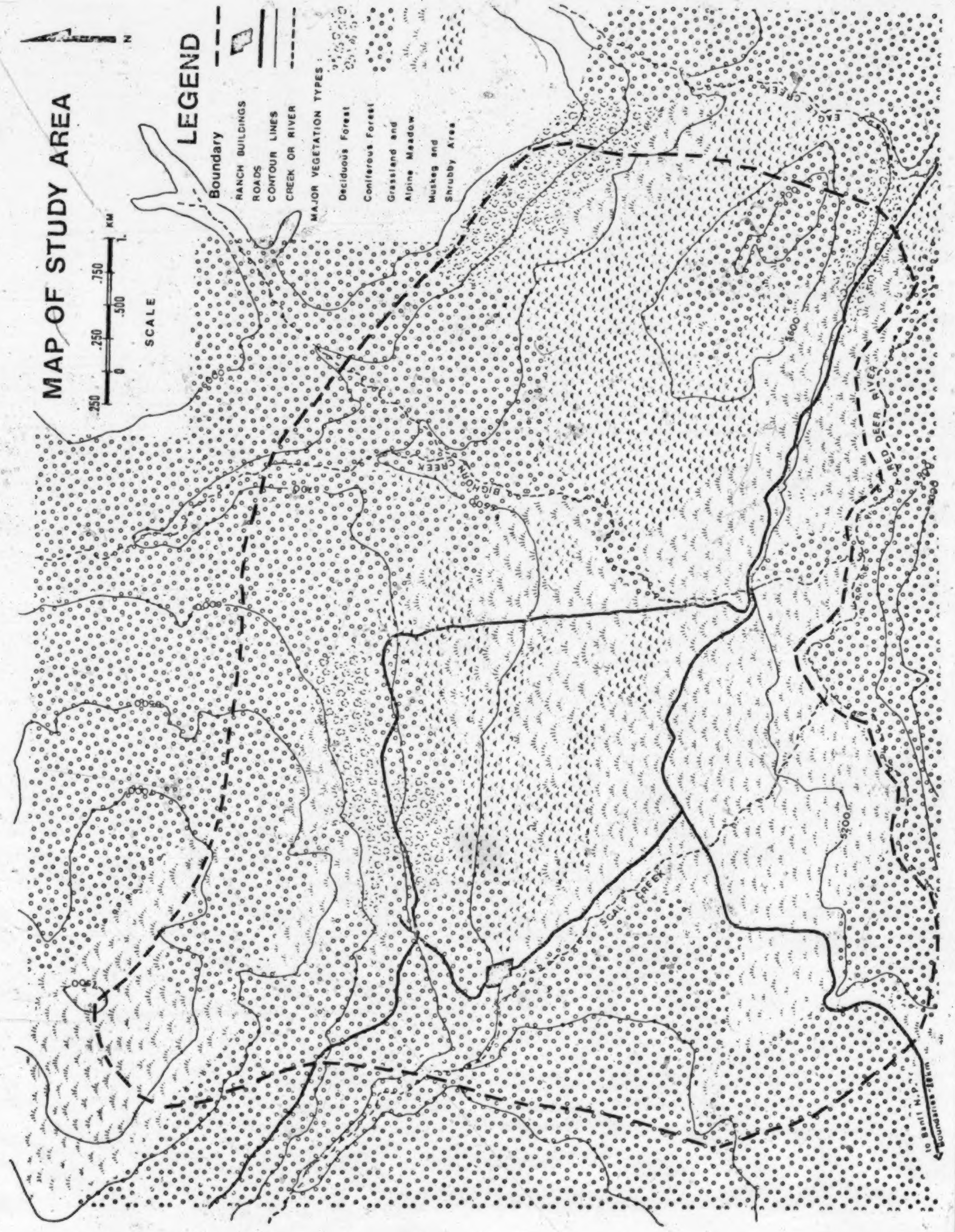
1.1. Choice of Study Area

The study area was chosen on the basis of its relatively 'natural' biotic conditions. Environmental diversity, high density of different ungulate species, and a clear pattern of seasonal movements were considered essential. From a logistic point of view, ease of access was also important. After having considered several sites, ranges adjacent to and on the Ya Ha Tinda Ranch were believed to be most suitable in spite of a large number of horses wintering on the area and of a relatively extensive hunting season. Although the impact of these two factors on wildlife habitat selection was unknown both factors could be considered during the study.

1.2. Physiography

The study was conducted on and in the vicinity of the central and eastern section of the Ya Ha Tinda Ranch (Figure 1.1). The area, located in the Red Deer River valley at 115°30'-36' W and 51°43'-47' N about 10 kilometers east of the eastern boundary of Banff National Park, embraces

Figure 1.1. Cover map of the study area, located approximately 10 km east of Banff National Park in central western Alberta.


MAP OF STUDY AREA
N
.250
0
.250
.500
.750
1
KM
SCALE
LEGEND
Boundary
RANCH BUILDINGS
ROADS
CONTOUR LINES
CREEK OR RIVER
MAJOR VEGETATION TYPES :
Deciduous Forest
Coniferous Forest
Grassland and
Alpine Meadow
Muskeg and
Shrubby Area
BIGHORN CREEK
EAGLE CREEK
RED DEER RIVER
SCALP CREEK
1600
1800
2000
2200
to Banff N.P. boundaries-10km

approximately 35 km² of which about 30 percent is covered by native grassland and alpine meadows, 55 percent by forest and 15 percent by shrubs and muskegs (Figure 1.2).

Elevation ranges from 1,550 m (5,100 ft) in the valley floor to 2,450 m (8,000 ft) in the surrounding mountains. The hummocky and rolling relief of the valley floor (15 km²), where about half of the study area lies, reflects a glacial origin. The presence of several types of landform is the result of the retreat of the ice towards the upland cirques on both the west and north side of the valley. Superficial glacial deposits are composed of an unsorted mixture of clay, silt, sand and gravel (McPherson, 1963). Soils are described as orthic black and eluviated black chernozem, orthic-regosol, orthic grey and brunisolic grey luvisol and peaty orthic humic gleysol (McGillis, 1977).

1.3. Vegetation

Most of the valley floor is covered by native grassland described as a modified Stipetosum comatae variant of the Festuco-Stipetum richardsoni association (Looman, 1969). The presence of this association is considered by Looman to be an "azonal occurrence" and it is accounted for by the existence of particular climatic conditions. Description of the grassland can be found in Scotter (1975) and McGillis (1977). Throughout the area shrubby cinquefoil

Figure 1.2. Panoramic view of part of the study area, looking (from a to d) east, south-east, south and south-west.

a.

b.

c.

d.

(Potentilla fruticosa L.) is associated with the grassland.

The rest of the valley floor is covered by sedge (Carex spp.) in moister places, by willow species (Salix glauca L. and Salix spp.) and/or dwarf birch (Betula glandulosa Michx.), depending on site factors, and by forests. Towards the mountains and on the slopes, white spruce (Picea glauca (Moench) Voss), lodgepole pine (Pinus contorta Loud. Var. latifolia Engelm.), quaking aspen (Populus tremuloides Michx.) and balsam poplar (Populus balsamifera L.) constitute the dominant trees.

1.4. Climate

The climate of the area is described by McGillis (1977) as continental, with warm summers and cold winters. The author reports the mean temperatures of January and July, the coldest and warmest months, to be about -10°C to -12°C and from 13°C to 16°C, respectively. The frost-free period is about 60 days and precipitation is 45 to 50 centimeters per year, most of which falls during the growing season (McGillis, 1977).

However, the micro-climate of the Ya Ha Tinda Ranch area can be highly variable. Data tabulated by Gates (1975) show from May 1972 to April 1973 higher precipitation in summer than winter with 5 and 42 percent of the summer precipitation (May-September) occurring in May and June, respectively. Conversely, from May 1973 to April 1974 the author reported higher precipitation in winter than in summer with only 19 and 15 percent of the summer precipitation (May-September) occurring in May and June. During both summers the warmest month was August (Gates, 1975).

Several reports on the late season elk hunt in the Ya Ha Tinda Ranch prepared by the Alberta Fish & Wildlife Division (1968-1976; Alberta Fish & Wildlife Division files) refer to weather observations made at the Environment Canada weather station situated at Mountain Aire Lodge which lies outside the valley 20 km to the east.

The present study indicates that the microclimate of Ya Ha Tinda Ranch valley is remarkably distinct. As a result of the effect of the surrounding mountains on air flows, the study area enjoys mild weather. Cloud cover does not develop to the extent that it does over the surrounding areas and western winds keep the grassland largely snow-free.

During the study from December 1975 to May 1976 a weather station was operated at the Ranch. Minimum and maximum temperatures and precipitation were recorded on each day of field work which amounted to about 15-20 days every month. In Figure 1.3 average minimum and maximum temperatures and in Table 1.1 average precipitation of each period are compared with the average minimum and maximum temperatures and precipitation recorded during the same periods at the Mountain Aire Lodge.

Figure 1.3. Average minimum and maximum temperatures for the Ya Ha Tinda Ranch valley and the Mountain Aire Lodge recorded during periods of field work.

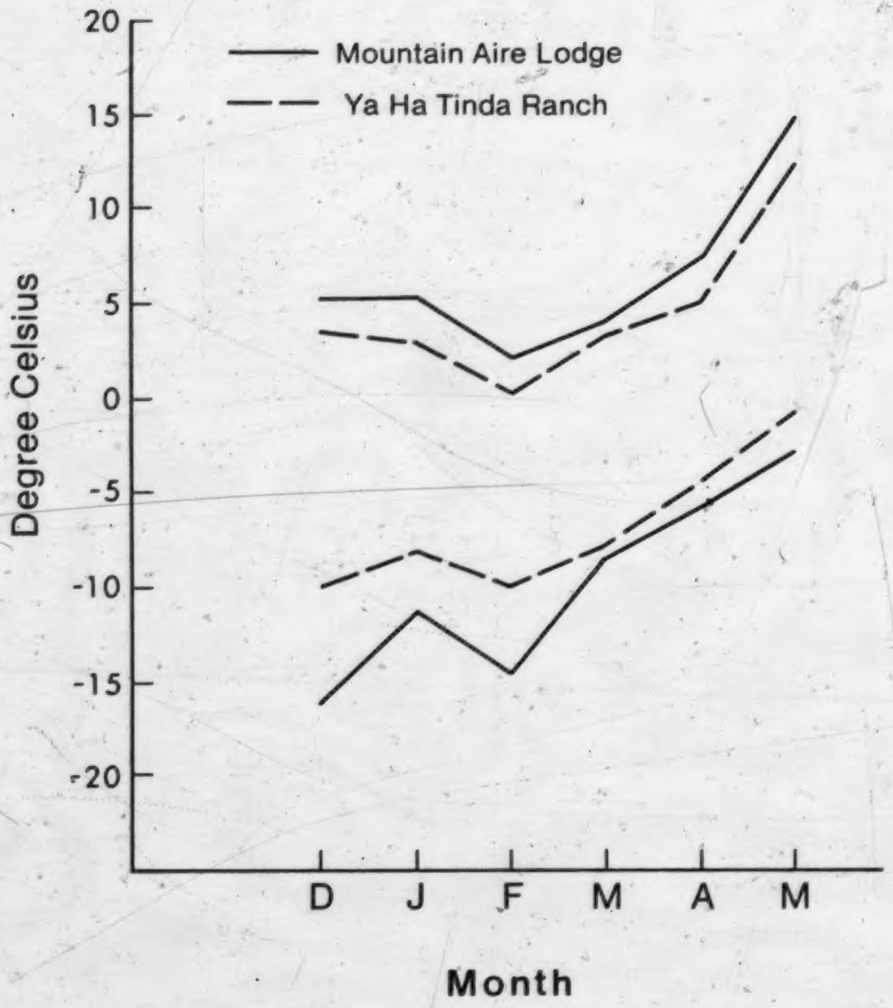

Mountain Aire Lodge
Ya Ha Tinda Ranch
Degree Celsius
20
15
10
5
0
-5
-10
-15
-20
D
J
F
M
A
M
Month

Table 1.1. Amount of precipitation (cm) recorded on the Ya Ha Tinda Ranch for periods of 15-20 days every month as compared with the amount of precipitation recorded during the same periods at the Mountain Aire Lodge. (Dec. 1975-May 1976).

	YA HA TINDA RANCH	MOUNTAIN AIRE LODGE
DECEMBER	.10	.20
JANUARY	.05	.05
FEBRUARY	.25	.86
MARCH	1.80	1.54
APRIL	2.49	2.61
MAY	.99	3.45
TOTAL	5.68	8.71

* Precipitation is expressed as "the sum of the total rainfall and the water equivalent of total snowfall" according to Environment Canada (1973).

The results show smaller temperature variations, particularly evident during the months of December, January and February, lower precipitation and generally a milder climate in the Ya Ha Tinda valley.

1.5. History and Animal Populations

At the present time Ya Ha Tinda Ranch is used by Parks Canada to pasture horses in winter and for horse breeding. These horses are used in summer by the Warden Service of the National Parks in Western Canada for backcountry movements and patrol. Until 1930, with the exception of the period 1911-1917, the ranch and the area surrounding were part of the Rocky Mountain Park and were considered to be "a strategic position in relation to wildlife" (Lothian, 1966). From 1905 until 1917 part of the ranch was leased by the Brewster Brothers of Banff for grazing up to about 300 horses and 50 cattle. From 1917 until the present time the ranch and surroundings have been used by Parks Canada as horse pasture. The average number of animals was 50 until 1960 (Lothian, 1966), and from then on approximately 200 in winter and 50 in summer (Scotter, 1975; S. Haugen, pers. comm.).

The whole area is an important winter and spring range for bighorn sheep and wapiti or elk. Mule deer and white-tailed deer (Odocoileus virginianus), according to local old timers, were common in the early 1930's. At the present time mule deer and white tailed deer use the ranch area mainly during spring and the total population is estimated at about 30-40 (pers. obs.).

Bighorn sheep use several slopes which surround the valley as winter and sometimes as summer range. Small bands are reported wandering around salt licks and occasionally grazing on the grassland in the Ranch area (Flook, 1957; this study). Gates (1975) reported two herds of about 60 and 50 animals wintering on the southwest-facing slopes north of Scalp creek and on the west-facing slopes near Eagle creek, respectively. During the present study (winter 1975-76) bighorn sheep were frequently observed also south of the Red Deer River. Because no winter movement of animals was observed between the three herds (also Gates, pers. comm.) they should be considered quite distinct. A conservative estimate of the total population from this study would be about 130.

The recorded presence of elk on and near the Ya Ha Tinda Ranch goes back to the early 1900's, however extensive use of the area as prime winter range is dated to the 1940's (Neave, 1970). From 1959 to the present the number of animals reported at any one time has ranged from 1,400-1,800 (April, 1961) to 399 (January, 1975) (Alberta Fish & Wildlife Division files). The numerous and widely contrasting 'counts' of the elk wintering on the Ya Ha Tinda area during last 20 years consist of estimates from occasional observers and ground or aerial surveys conducted at different dates and times and with different weather conditions and observers. For this reason no meaningful comparison can be made from year to year. Nevertheless, it appears that the number of elk that have wintered on the Ranch area in the last few years is lower than it was in the 1960's. During the winter of 1975-76 the highest number of elk recorded at one time in the Ya Ha Tinda Ranch was 380 animals.

From 1969 until 1975, with the exception of 1972, in response to a presumed overpopulation of elk in the Ya Ha Tinda Ranch, special hunting seasons were conducted in January and February on the ranch and surrounding areas. An average of 112 elk per special season, mostly cows and calves, were harvested. In 1976, when this study was being conducted, the special season was limited to bulls.

CHAPTER TWO

RESOURCE BASE

2.1. Introduction

Most biologists have used vegetation analysis and classification as means to evaluate and quantify wildlife habitats. However, the ways in which these have been carried out often varied remarkably from one study to another. Factors such as background of the researcher and objectives of the study have played an important role in determining approaches and techniques. Also, the recent widespread use of computer facilities that enables the handling of large sets of data and the application of sophisticated statistics as objective methods of analysis have greatly increased the variety of classifications that can be obtained.

During the last few years there has been an increasing tendency among wildlife investigators to adopt approaches and techniques generally used by plant sociologists. Several habitat classifications have been based on their vegetational attributes whereas others have included site (i. e., slope, aspect, etc.) and/or soil characteristics (Thilenius, 1972; Hoffman and Alexander, 1976; Severson and Thilenius, 1976). The underlying assumption is that the selection of habitat by wild ungulates is determined mainly by the floristic composition of a site. This approach does not consider the 'edge effect' (Odum, 1971; Lamprey, 1963) nor the importance of 'patchy environments' (Wiens, 1976). The latter being a mosaic of vegetation communities where each one considered by itself would have little significance for the animal. Further, as pointed out by Moen (1973), a classification of wildlife habitats based on plant taxonomy "may be adequate from a humanistic, systematic point of view" (Moen, 1973: p. 28) but it does not take into consideration what an animal actually experiences.

In the present study the basic conceptual framework of Fosberg's structural system of vegetation classification (Fosberg, 1961) was adopted. Specifically emphasis was placed on Fosberg's concept of structure as described by Mueller-Dombois and Ellenberg (1974) as 'the arrangement in space of the plant biomass'. The attributes upon which the classification of vegetation types was to be based upon were subjectively selected as potential determinants of ungulate distribution and considered to satisfy basic requirements of the animals such as predation avoidance, feeding and thermoregulation. Detailed floristic analysis was intentionally avoided. Soil and locational features were not incorporated into the classification. Because the objective of the study was limited to the analysis of spatial and behavioral patterns of wild ungulates no data was recorded of their food habits.

The rationale behind the type of vegetation classification adopted is the belief that habitat selection of gregarious and mobile wild ungulates is a very complex response to a large number of factors whose understanding is made more difficult by the fact that animals are sensitive to very different sensory stimuli from man. Therefore it cannot be described simplistically by differences in floristic composition from one site to another.

2.2. Methods

2.21. Field procedures

Identification and mapping of the vegetation types began during the summer of 1975, after an extensive ground survey, and was continued during the summer of 1976. The vegetation was first subdivided on the basis of its gross compositional features (Fosberg, 1961) into four major types: forests, shrubby areas, wet meadows and open grassland. This preliminary stratification was followed by extensive systematic survey and sampling in each major type. Depending on the heterogeneity of the area sampled, a combination of transects and/or randomly distributed quadrats was used (Oosting, 1956; Shimwell, 1973). Each quadrat, in both cases, consisted of three nested plots. A 1 x 1 m plot was used to obtain figures for the herbaceous layer, a 4 x 4 m plot for shrubs, and a 10 x 10 m plot for trees. Grasslands were not sampled since their floristic composition already had been reported by several authors (Looman, 1969; Scotter, 1975; Gates, 1975; McGillis, 1977).

The vegetation characteristics measured in each sampling location (quadrats) are listed in Tables 2.1 and 2.2. Forest structure was considered adequately described by tree density and basal area (BA). Cover was not estimated since it was regarded as related to both density and basal area. Trees less than 1.5 m high were arbitrarily classified as regeneration. Shrub density and cover figures were obtained by recording the number of stems and their approximate diameter for all species occurring in a 16 sq m quadrat. From the diameter of each plant its cover was computed and the total value for a species was divided by the size of the quadrat and expressed as a percentage. For the herb layer, forbs, grasses and grasslike plants, cover of dominant species was estimated in 1 sq m quadrats according to Oosting (1956). Sixty-two and forty-seven quadrats were sampled in forest and shrub areas, respectively.

2.22. Analytical techniques

Although during the field work a preliminary empirical classification of forest and shrub areas was evolved, in order to achieve a more objective classification

Table 2.1. Vegetation characteristics used to classify forest types.

TREES	
Pinus contorta Loud. *Var. latifolia* Engelm.	Density
" " " " " "	Basal area
" " " " " "	Regen. density
Picea glauca (Moench) Voss	Density
" " " "	Basal area
" " " "	Regen. density
Populus tremuloides Michx.	Density
" " "	Basal area
" " "	Regen. density
Populus balsamifera L.	Density
" " "	Basal area
" " "	Regen. density
SHRUBS	
Betula glandulosa Michx.	Cover
" " "	Density
Salix glauca L.	Cover
" " "	Density
Potentilla fruticosa L.	Cover
" " "	Density
Salix spp.	Cover
" "	Density
Shepherdia canadensis (L.) Nutt.	Cover
" " " "	Density
Rosa woodsii Lindl.	Cover
" " "	Density
Arctostaphylos uva-ursi (L.) Spreng.	Cover
GRASSES AND GRASSLIKE PLANTS	
Total grasses	Cover
Elymus innovatus Beal	Cover
Festuca scabrella Torr.	Cover
Sedge (*Carex* spp.)	Cover
OTHERS	
Moss	Cover
Total forbs	Cover

Table 2.2. Vegetation characteristics used to classify shrubland types.

SHRUBS	
Betula glandulosa Michx.	Cover
" " "	Density
Salix glauca L.	Cover
" " "	Density
Potentilla fruticosa L.	Cover
" " "	Density
Salix spp.	Cover
" "	Density
Shrub height class 1 (30-60 cm)	Density
" " class 2 (60-90 cm)	Density
" " class 3 (90 cm and over)	Density
Arctostaphylos uva-ursi (L.) Spreng.	Cover
GRASSES AND GRASSLIKE PLANTS	
Total grasses	Cover
Elymus innovatus Beal	Cover
Festuca scabrella Torr.	Cover
Sedge (*Carex* spp.)	Cover
OTHERS	
Total forbs	Cover
Populus tremuloides Michx.	Regeneration
Picea glauca (Moench) Voss	Regeneration

Principal Component Analysis and Cluster Analysis were applied. The desirability of using different techniques in processing data has been noted by Williams (1971). The analysis was carried out with an AMDAHL 470V/6 computer in operation at the University of Alberta, using the CLUSTAN IC program developed by Wishart (1975) of University College, London.

Principal Component Analysis (PCA) is a technique which is being used increasingly in ecological studies as a tool for reducing a complex set of data to a simpler one. This is accomplished by constructing a set of new variables (factors or components) which account for the interrelations in the data. The extracted components are orthogonal (uncorrelated) to each other and each accounts for a portion of the variance (eigenvalues) not accounted for by the other. Eigenvectors indicate the degree to which the original variables are associated with each component.

Wishart (1975) defines Cluster Analysis as a "...modern statistical method of partitioning an observed sample population into disjoint or overlapping homogeneous classes to produce an operational classification". Among several Cluster Analysis techniques available in the CLUSTAN IC program, two clustering procedures were used: HIERARCHY and RELOCATE.

1) Procedure HIERARCHY fuses, by "...combinatorial transformation of the similarity matrix..." (Wishart, 1975), individuals and clusters which are most similar. The

method requires computation of a similarity matrix.

2) Procedure RELOCATE, starting from K clusters of N individuals, removes one individual at a time and computes its similarity with all the K clusters. If the similarity with another cluster is greater than the similarity with the parent cluster, the individual will be relocated to the new cluster.

Using procedures HIERARCHY and RELOCATE, Ward's method of the least increase in the error sum of squares was adopted as the coefficient of similarity. With the procedure RELOCATE, ten random clusters of quadrats were selected as a starting point.

According to Wishart (1975), similar results achieved by different procedures are an indication of a robust classification.

Cluster Analysis with the CLUSTAN IC program has been recently applied by Stocker _et al_. (1977) in classifying deer habitat types in southern Ontario.

In this study the analysis was carried out for the set of variables listed in Tables 2.1 and 2.2.

2.3. Results and Discussion

The two techniques used in classifying the vegetation differ in approach. Principal Component Analysis considers the variations among the quadrats as continuous whereas Cluster Analysis groups quadrats in discrete associations on the basis of their similarity. Although different, in ecological studies both techniques complement each other (Clifford and Stephenson, 1975). The analysis was carried out for forest and shrub areas separately.

2.31. Forest classification

Using Principal Component Analysis 32 factors were extracted. Figures 2.1, 2.2 and 2.3 show the distribution of sampled quadrats plotted respectively on Factor I against Factor II, Factor I against Factor III, and Factor II against Factor III. These three factors accounted for a total of 50 percent of variance. Factor I was positively correlated with white spruce density, _Salix_ spp. density and moss cover, while negatively correlated with aspen BA, _Elymus innovatus_ cover and total grass cover. Factor II was positively correlated with _Salix glauca_ cover, _Salix glauca_ density and _Salix_ spp. density, while negatively correlated with lodgepole pine density and lodgepole pine BA. On the basis of these two factors a first separation between deciduous and coniferous forests and between pine and spruce communities, along Factor I and Factor II respectively, takes place (Figure 2.1).

The contribution of Factor III to the classification is more difficult to assess. This factor was positively correlated with _Betula glandulosa_ cover, _Betula glandulosa_ density and rough fescue cover, and negatively correlated

Figure 2.1. Distribution of forest sampling sites (quadrats) based on their loading on Factors I and II.

Figure 2.2. Distribution of forest sampling sites (quadrats) based on their loading on Factors I and III.

Figure 2.3. Distribution of forest sampling sites (quadrats) based on their loading on Factors II and III.

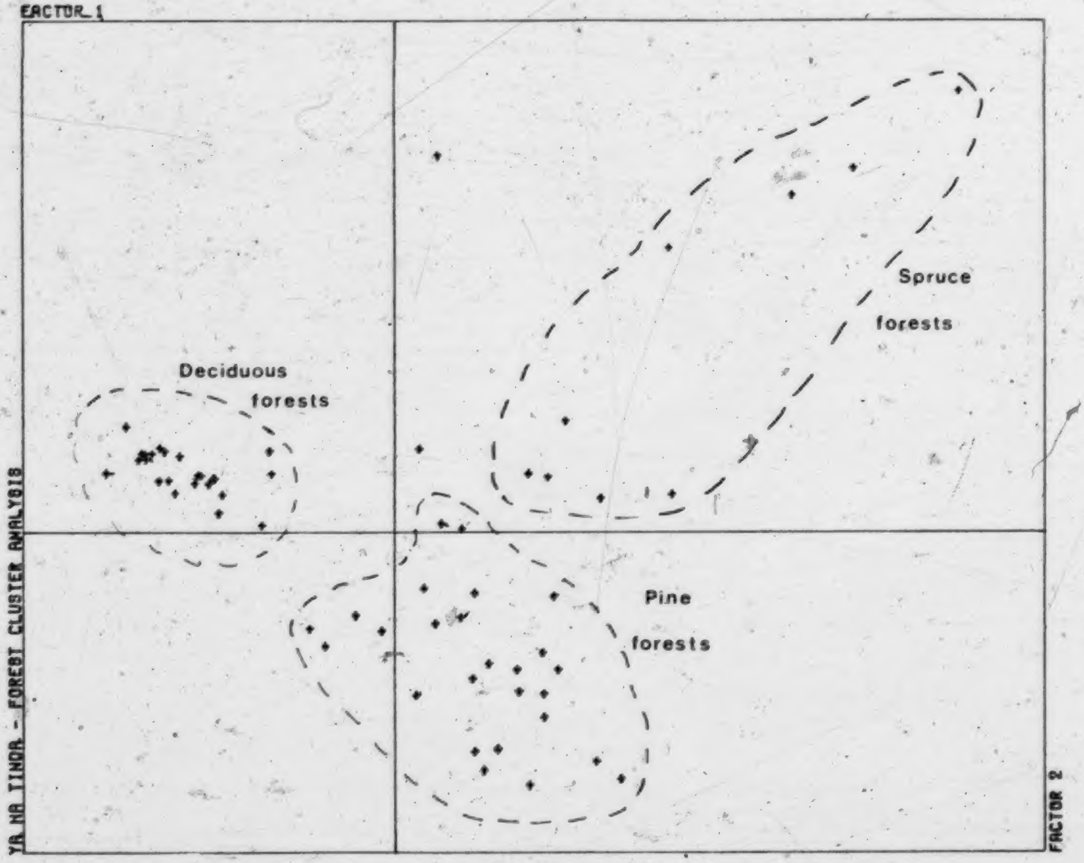


Figure 2.1.

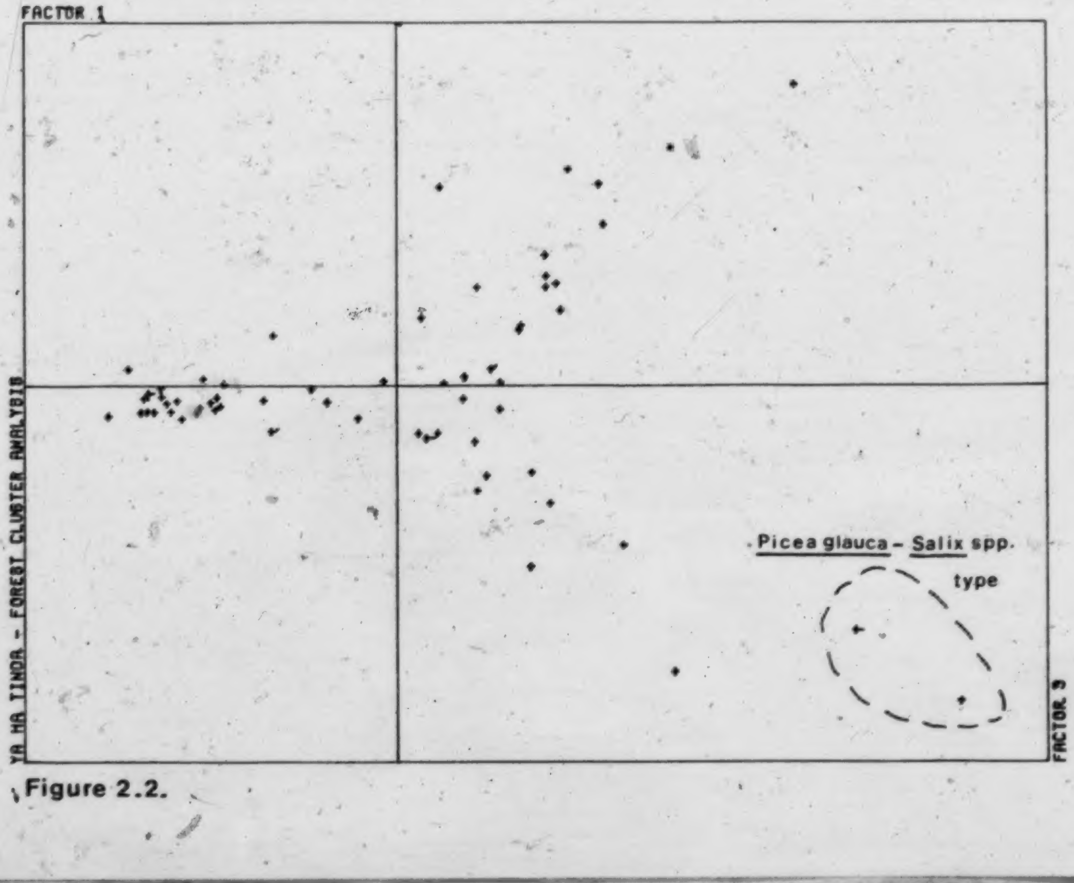


Figure 2.2.

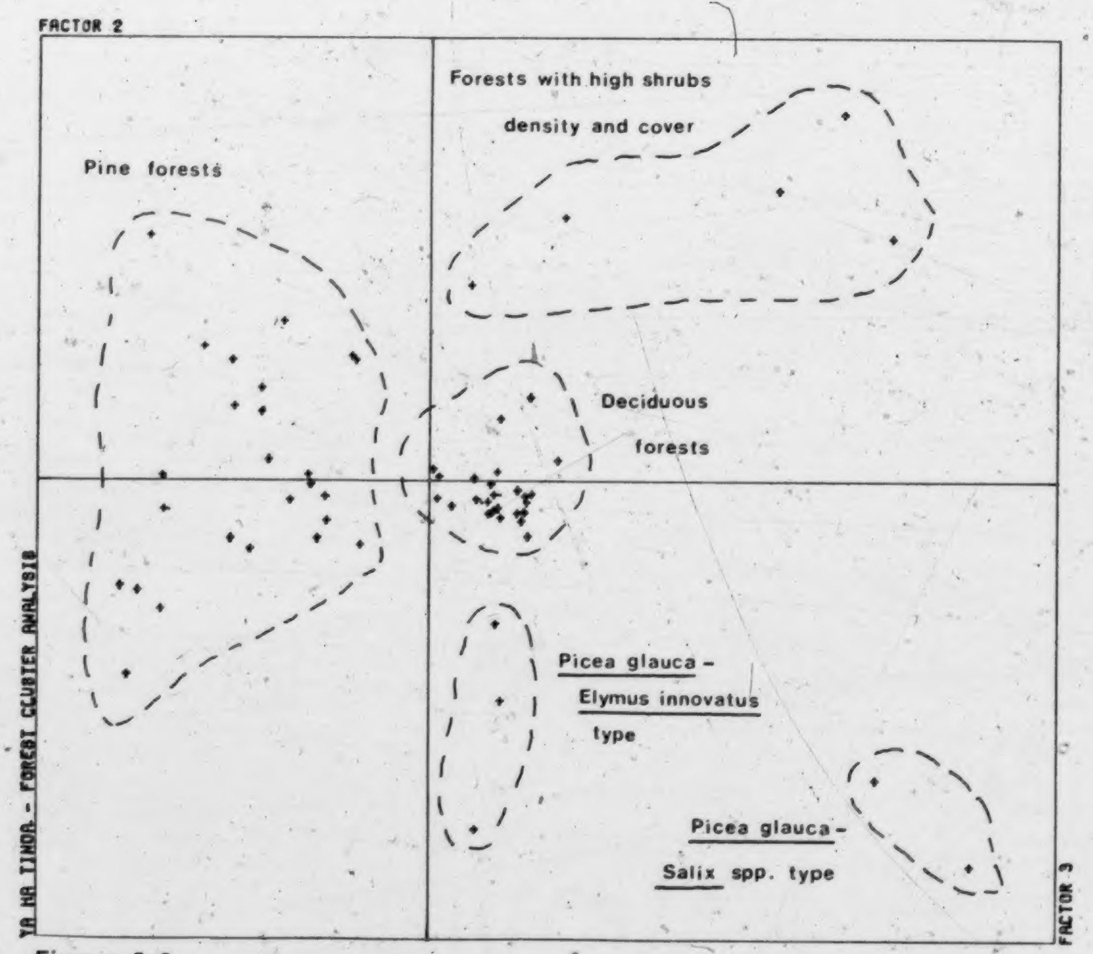

FACTOR 2
Forests with high shrubs density and cover
Pine forests
Deciduous forests
Picea glauca - Elymus innovatus type
Picea glauca - Salix spp. type
FACTOR 3
YA HA TINDA - FOREST CLUSTER ANALYSIS

Figure 2.3.

with white spruce BA and moss cover. In Figure 2.2 a discrete cluster of two quadrats can be observed. The two quadrats were sampled in an old, dense spruce forest with high Salix spp. density and cover, and moss cover. Their location in the figure reflects the positive correlation of Factor I with Salix spp. and spruce density and the negative correlation of Factor III with spruce basal area and moss cover. Figure 2.3, where Factor III is plotted against Factor II, shows separation along Factor III between spruce communities and forest communities with high densities and cover of shrubs due to the concomitant positive correlation of both factors with density and cover of different shrubs species. In the same figure, two types of spruce forest and pine from deciduous communities can be recognized.

The results obtained through the interpretation of the first three factors, although ecologically interesting, seem of limited practical use for classifying forest types. Possibly the clusters of pine forests, deciduous forests and high density shrubs forests (Figure 2.3) could be broken down by considering the remaining factors (IV,V,...,n) and plotting one against the others. However, this would require an inordinate amount of effort. In this aspect Cluster Analysis appears to be a more adequate technique for a practical classification of forest types.

In Figure 2.4, the dendrogram generated with procedure HIERARCHY is represented. The horizontal line subjectively drawn at a similarity coefficient of 3.4 marks

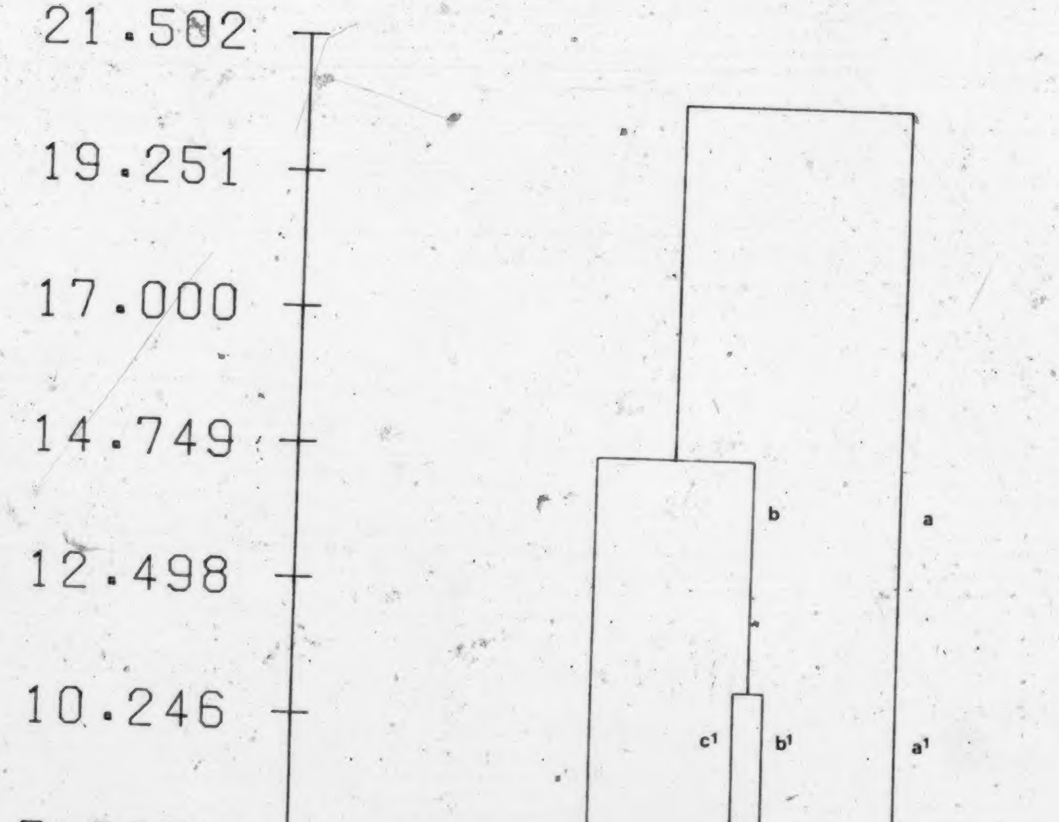
Figure 2.4. Dendrogram showing classification of 62 forest sampling locations (quadrats) into clusters obtained by using Ward's method. The horizontal line indicates the similarity level at which ten clusters represent ten forest types clearly recognizable in the field. The letters a, b, c, and a^1, b^1, c^1, d^1, e^1, refer to discrete clusters obtained previously from the interpretation of the first three factors of Principal Component Analysis (Figures 2.1 and 2.3).

From Figure 2.1:

a = Deciduous forests
b = Spruce forests
c = Pine forests

From Figure 2.3:

a^1 = Deciduous forests
b^1 = *Picea*-*Salix* spp. type
c^1 = Forests with high shrub density and cover
d^1 = *Picea glauca*-*Elymus innovatus* type
e^1 = Pine forests



FOREST CLASSIFICATION DENDROGRAM

ten clusters of quadrats which represent ten forest types clearly recognizable in the field. Any other group of clusters at a lower similarity coefficient would not constitute a realistic classification of forest types according to the concepts defined earlier and would be inadequate for the objective of this study. On the dendrogram (Figure 2.4) the letters a, b, c, and a', b', c', d', e', refer to discrete clusters obtained previously from the interpretation of the first three factors of PCA (Figures 2.1 and 2.3, respectively).

Ten clusters remarkably similar to those obtained with procedure HIERARCHY were achieved with procedure RELOCATE. Four quadrats (6.4% of the number analyzed) were assigned to two different clusters. However, the discrepancy, though difficult to explain, does not affect the classification as a whole nor the characteristics of each cluster. Therefore a classification based on ten clusters was adopted. The respective ten forest types were named according to the predominant species present. Their major vegetational and structural characteristics are listed in Table 2.3. Descriptions can be found in the summary table (Table 2.5, page 42).

2.32. Shrubland classification

Using Principal Component Analysis, six ecologically interpretable factors were extracted. Figures 2.5 and 2.6

Table 2.3. Major vegetational and structural features of forest types classified within the study area.

	FOREST TYPES									
	A	B	C	D	E	F	G	H	I	J
No. of sampling locations	3	2	4	6	10	3	9	17	7	1
Pinus contorta										
Mean density (n/100m²)	0	0	2	15	14	81	10	1	1	0
Mean BA (cm²)	0	0	200	3,000	3,100	5,200	1,000	100	200	0
Mean reg. density (n/100m²)	0	0	2	0	1	1	24	0	0	0
Picea glauca										
Mean density (n/100m²)	32	29	5	2	4	0	3	1	0	0
Mean BA (cm²)	4,800	3,200	700	600	700	0	200	100	0	0
Mean reg. density (n/100m²)	10	2	4	8	5	7	24	0	0	0
Populus tremuloides										
Mean density (n/100m²)	0	0	0	3	0	0	0	29	22	0
Mean BA (cm²)	0	0	0	100	0	0	0	3,900	2,100	0
Mean reg. density (n/100m²)	0	0	0	8	12	0	0	38	22	550
Populus balsamifera										
Mean density (n/100m²)	0	0	0	4	1	0	0	1	8	18
Mean BA (cm²)	0	0	0	300	100	0	0	100	1,400	600
Mean reg. density (n/100m²)	0	0	0	3	4	0	2	2	7	68
Shepherdia canadensis										
Mean density (n/100m²)	2	6	10	25	6	4	11	1	2	0
Mean cover (%)	.11	.32	.01	14.28	1.67	1.03	1.52	.30	.41	0
Salix glauca										
Mean density (n/100m²)	7	5	34	0	7	1	6	1	0	93
Mean cover (%)	.46	6	8.23	0	.53	.01	.48	.03	0	12.88
***Salix* spp.**										
Mean density (n/100m²)	0	93	19	0	1	0	0	0	0	0
Mean cover (%)	0	21.54	2.59	0	.10	0	0	0	0	0
Betula glandulosa										
Mean density (n/100m²)	1	9	45	0	0	0	3	0	0	0
Mean cover (%)	.12	.09	19.78	0	0	0	1.07	0	0	0
Potentilla fruticosa										
Mean density (n/100m²)	1	0	85	0	4	0	74	6	7	0
Mean cover (%)	.01	0	.26	0	.07	0	.78	.07	.13	0
***Rosa* spp.**										
Mean density (n/100m²)	1	0	0	3	1	0	0	2	18	0
Mean cover (%)	.01	0	0	.05	.02	0	0	.01	.15	0
Arctostaphylos uva-ursi										
Mean cover (%)	11.67	0	7.50	29.17	3.30	26.67	37.89	.88	0	0
Elymus innovatus										
Mean cover (%)	38.33	0	2.50	35.00	42.90	23.33	14.22	79.41	82.86	60.00
Festuca scabrella										
Mean cover (%)	0	0	55.00	10.83	24.00	11.67	31.67	6.18	5.00	5.00
Total forbs										
Mean cover (%)	3	2.50	13.75	18.70	14.60	6.00	7.56	48.52	34.28	25.00
Moss										
Mean cover (%)	83.33	92.50	0	.17	.50	32.00	0	0	0	0
Sedge										
Mean cover (%)	0	25.00	0	0	0	0	0	0	0	0

LIST OF FOREST TYPES :

A = *Picea glauca-Elymus innovatus*
B = *Picea glauca-Salix* spp.
C = *Picea glauca-Betula glandulosa*
D = *Pinus contorta-Shepherdia canadensis*
E = *Pinus contorta-Elymus innovatus*
F = *Pinus contorta*-moss
G = *Pinus contorta-Picea glauca*
H = *Populus tremuloides-Elymus innovatus*
I = *Populus tremuloides-P. balsamifera*
J = *Populus balsamifera-Salix* spp.

Figure 2.5. Distribution of shrub sampling locations (quadrats) based on their loading on Factors I and II.

Figure 2.6. Distribution of shrub sampling locations (quadrats) based on their loading on Factors II and III.

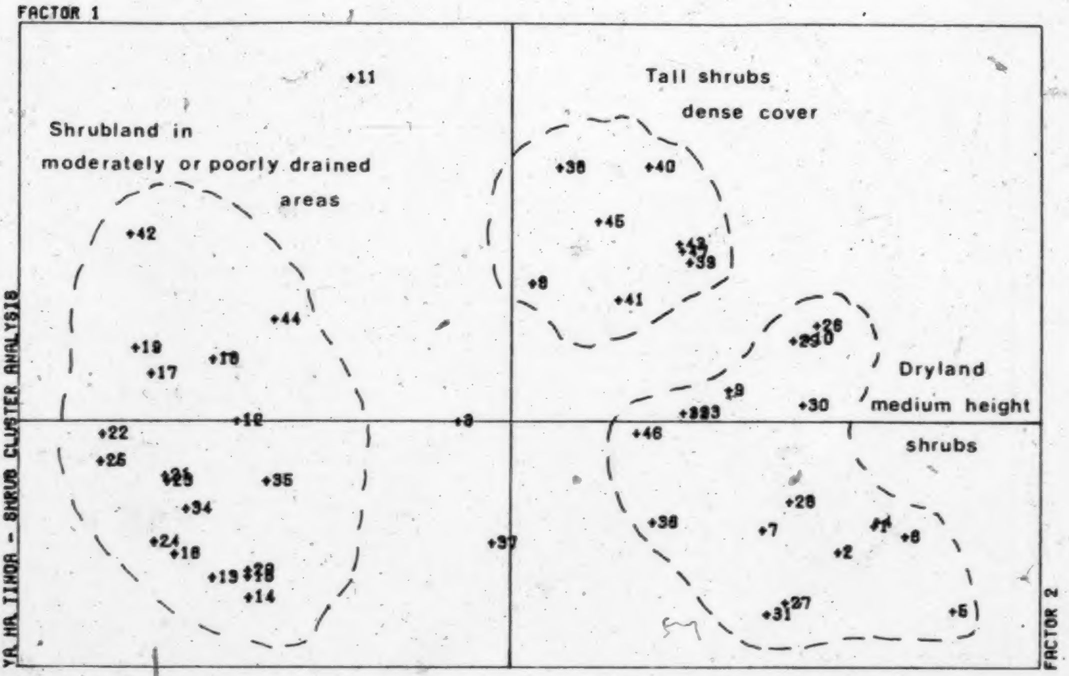


Figure 2.5.

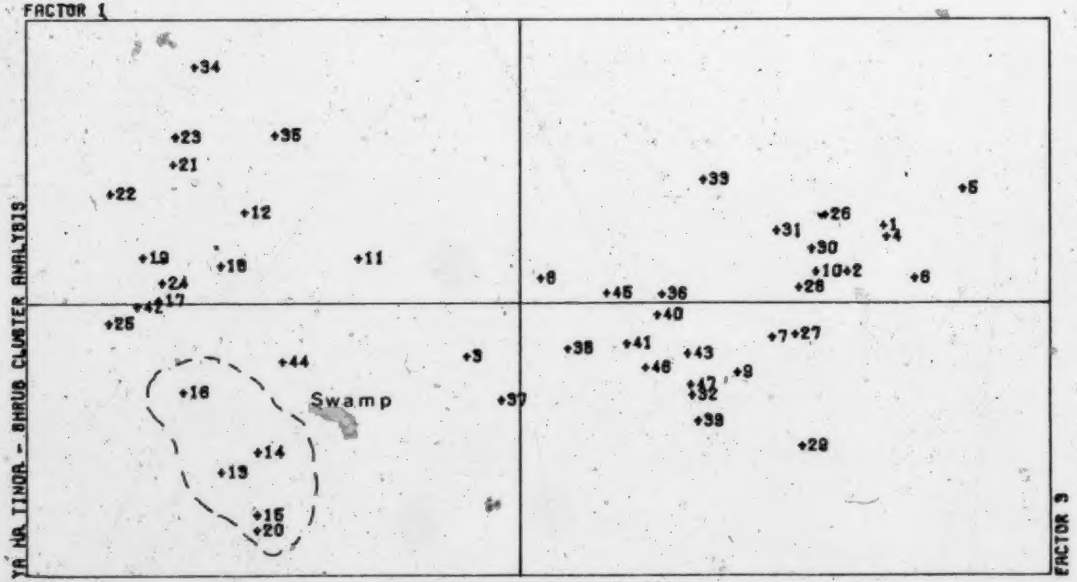


Figure 2.6.

show the distribution of sampled quadrats plotting Factor I against Factor II and Factor I against Factor III, respectively. Factor I, which accounted for 35 percent of the total variance, was positively correlated with total grass cover, rough fescue cover and total forbs cover, while negatively correlated with sedge cover and Salix spp. density. This factor can be considered as representing a dry-moist gradient along which a preliminary sorting of sites into two discrete clusters was achieved (Figure 2.5).

Factors II and III accounted respectively for 14 and 11 percent of the total variance. Their ecological interpretation is somewhat more difficult. Factor II was positively correlated with Betula glandulosa cover, Salix glauca cover and density of tall shrubs (90 cm and higher), while negatively correlated with Betula glandulosa density, Potentilla fruticosa density and sedge cover. Factor III was positively correlated with Betula glandulosa density, Potentilla fruticosa density and density of short shrubs (30-60 cm), while negatively correlated with Salix glauca density and aspen regeneration density. Figures 2.5 and 2.6 show the separation of two discrete clusters of quadrats, one along Factor II and one along Factor III respectively. On the basis of the degree to which the original variables were associated with Factor II and III the two clusters were interpreted as representing sites characterized by tall shrubs and dense shrub cover in relatively dry areas (Figure 2.5) and wet meadows with low growing Salix spp. (Figure

2.6).

The four clusters achieved through the interpretation of the first three factors constituted an acceptable classification of shrubland types. A more refined classification would be unrealistic and hardly recognizable in the field.

Identical results were obtained using Cluster Analysis, procedure HIERARCHY. The dendrogram of Figure 2.7 at a similarity coefficient of 6.0 shows the same four clusters obtained with Principal Component Analysis.

Procedure RELOCATE produced slightly different results. The disparity between the two classifications seems limited to the addition of five quadrats to a cluster previously characterized by procedure HIERARCHY as composed by only eight quadrats. This discrepancy could be possibly attributed to an underlying continuity existing among the quadrats separated in two discrete clusters along Factor II mainly on the basis of the height and cover of shrub species (Figure 2.5). However, since similar classifications were achieved by means of both Principal Component Analysis and Cluster Analysis, procedure HIERARCHY, the four clusters as defined by the latter were adopted. The respective four types of shrubland were identified and named according to their characteristic structural features. Table 2.4 shows vegetational and structural features while a detailed description is found in the summary table (Table 2.5, page 42).

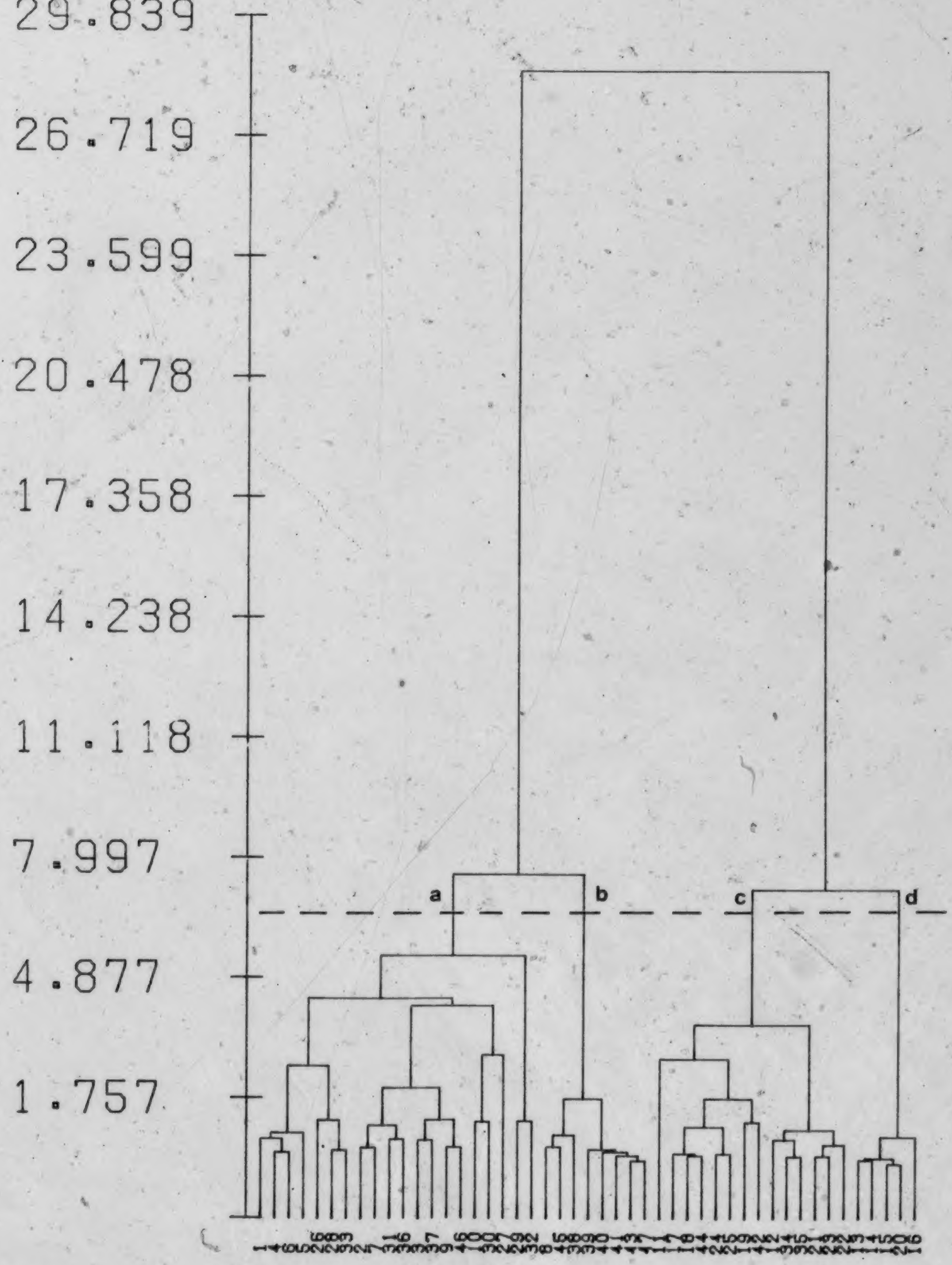
Figure 2.7. Dendrogram showing classification of 47 shrub sampling locations (quadrats) into clusters obtained by using Ward's method. The horizontal line indicates the similarity level at which four clusters represent four shrubland types clearly recognizable in the field. The letters a, b, c, and d refer to discrete clusters obtained previously from the interpretation of the first three factors of Principal Component Analysis (Figures 2.5 and 2.6).

From Figure 2.5:

a = Dryland medium height shrubs
b = Tall shrubs, dense cover
c = Shrubland in moderately or poorly drained areas

From Figure 2.6:

d = Swamp



SHRUBLAND CLASSIFICATION DENDROGRAM

Table 2.4. Major vegetational and structural features of shrubland types classified within the study area.

	SHRUBLAND TYPES			
	A	B	C	D
No. of sampling locations	20	8	14	5
Tall shrub classes				
1 : 30-60 cm				
Mean density (n/sqm)	1.42	.71	1.23	.38
2 : 61-90 cm				
Mean density (n/sqm)	.57	.68	.73	0
3 : 91 cm +				
Mean density (n/sqm)	.06	.55	.29	0
Salix glauca				
Mean density (n/sqm)	1.19	.87	.43	1.09
Mean cover (%)	24.30	36.40	24.42	1.48
Salix spp.				
Mean density (n/sqm)	.18	.29	.93	.76
Mean cover (%)	.55	2.03	6.37	.80
Betula glandulosa				
Mean density (n/sqm)	.69	.46	.65	.48
Mean cover (%)	20.20	50.80	36	1.70
Potentilla fruticosa				
Mean density (n/sqm)	1.15	.32	.57	0
Mean cover (%)	5.60	.67	1.92	0
Arctostaphylos uva-ursi				
Mean cover (%)	35.20	50.81	1.78	0
Elymus innovatus				
Mean cover (%)	17.35	6.87	32.07	0
Festuca scabrella				
Mean cover (%)	68.70	75.62	6.14	0
Total forbs				
Mean cover (%)	21	13.75	2.57	.40
Sedge				
Mean cover (%)	2.50	0	70.78	91

LIST OF SHRUBLAND TYPES :

A = Dryland shrubs
B = Tall shrubs
C = Shrubs-swamp
D = Swamp

2.33. Grassland classification

2.331. Lower grasslands

In spite of local floristic variations the ranch grassland was arbitrarily considered as a single discrete vegetation type. This assumption, hardly admissible in vegetation studies, was dictated by the inherent difficulties in delimiting and recognizing from a distance a more detailed classification based on differences in floristic composition. At the end of this study it was observed that the assumption made was acceptable since the animals used the grassland with a relatively uniform pattern altered only by other identified factors (Chapter 3).

2.332. Open mountain ranges

During this study only the ranges located north of the ranch grassland (Figure 1.1) were considered. Following Gates' description (1975) of their vegetational characteristics the open mountain slopes were classified into two types, low and high elevation ranges.

2.4. Summary

Within the Ya Ha Tinda Ranch study area eighteen vegetation types were classified. Their description is found in Table 2.5. In this table two vegetation types that were identified at the conclusion of forest analysis (*i. e.*, *Picea glauca*-*Betula glandulosa* and *Populus balsamifera*-*Salix* spp.) were considered as shrubland types because of their highly developed shrub stratum. In addition one more type was included representing disturbed sites (*e. g.*, road-sides). Its vegetational characteristics were not quantified due to their variability from site to site.

Table 2.5. Description of vegetation types classified within the study area.

Vegetation Type	Description
Open Mountain Ranges	
1. High elevation ranges	Subalpine grasslands located at elevation above 2,074 meters. *Elymus innovatus* is the predominant grass species. Sedges make up 40% of the floristic composition. *Arctostaphylos uva-ursi* is the primary shrub. (From Gates, 1975).
2. Low elevation ranges	Located between 1,922 and 2,074 meters of elevation. The dominant grass species in descending order of frequency of occurrence are *Agropyron dasystachyum* (13%), *Calamagrostis purpurascens* (11%), and *Koeleria cristata*. Sedge make up 10% of the floristic composition. (From Gates, 1975).
Lower Grasslands	
3. Grassland	Native grassland occupying a large section of the valley floor. *Festuca scabrella* is the dominant grass species. *Koelaria cristata*, *Poa interior* and *Elymus innovatus* are also present. Their relative cover varies from site to site. In moister places sedge species (*Carex* spp.) occur. The shrub stratum is dominated by *Potentilla fruticosa*. (From Scotter, 1975 and McGillis, 1977).

.../continued

Shrubland Types

4. Dryland shrubs	Common on dry to well drained sites. Moderately dense shrub stratum (total mean cover 44%) of medium height (30-80 cm). *Salix glauca* is the most prominent shrub species (1.19 plants/sqm, mean cover 24%). *Potentilla fruticosa* (1.15 plants/sqm, mean cover 5%) and *Betula glandulosa* (.69 plants/sqm, mean cover 20%) also are common. The herbs stratum is dominated by *Festuca scabrella*, followed by *Elymus innovatus*.
5. Tall shrubs	This type occurs in moderately drained sites. It is distinguished from the previous type by a dense (total mean cover 90%), tall (90-150 cm) shrub stratum of *Betula glandulosa* and *Salix glauca*, with cover of 50 and 36% respectively. *Salix glauca* occurs more frequently (mean density .87 plants/sqm) than *Betula glandulosa* (mean density .46 plants/sqm). *Arctostaphylos uva-ursi* is common (mean cover 51%). The herb stratum is dominated by grass species (*Festuca scabrella* dominant). When the tall shrub type occurs in poorly drained sites grasses are replaced by sedge species.
6. Shrub-swamp	It frequently occurs on the periphery of the swamp type, but it can be also found in forest openings and in poorly drained areas. This type is identified by a relatively dense shrub stratum (total mean cover 72%) of medium height (30-80 cm). *Betula glandulosa* is the dominant shrub species. *Salix glauca*, *Salix* spp. and *Potentilla fruticosa* are present. The herb stratum is composed mostly by sedge (total mean cover 70%).

.../continued

7. Swamp	This vegetation type, frequent in the study area, is restricted to mesic sites and depressions. It is characterized by a low cover (total mean cover 10%) of a prostrate shrub stratum and by a dense herb stratum of sedge. *Salix glauca* and *Salix* spp. are the most common shrub species.
8. Forested shrubland (*Picea*-*Betula*)	Common at the edge of coniferous forests. This shrubland type is characterized by the presence of a tree stratum composed by *Picea glauca* (mean density 5 stems/100 m²; mean BA 700 cm²) and *Pinus contorta* (mean density 2 stems/100 m²; mean BA 200 cm²). It has a dense shrub stratum of *Betula glandulosa* (mean cover 8%, mean density .34 plants/sqm). *Shepherdia canadensis* and *Potentilla fruticosa* are also common. The herb layer is mostly represented by *Festuca scabrella* (mean cover 55%).
9. Thickets	Tall, very dense thickets of *Salix* spp. (mean density .93 plants/sqm) and of *Populus balsamifera* and *Populus tremuloides* regeneration (mean density .68 and 5.50 plants/sqm, respectively). The tree stratum is composed by *Populus balsamifera* (mean density 18 plant/100 m²). This type is patchily present along streams and in deciduous forests.

.../continued

Forest Types

Deciduous forests	
10. *Populus tremuloides*-*Elymus innovatus*	*Populus tremuloides* dominated forest type (mean density 29 plants/100 m^2, mean BA 3900 cm^2). Also occasionally present, in decreasing order, are *Populus balsamifera*, *Pinus contorta* and *Picea glauca*. In the shrub stratum *Salix glauca*, *Salix* spp., *Shepherdia canadensis*, *Potentilla fruticosa* and *Rosa* spp. are present. *Elymus innovatus* dominates the herb stratum (mean cover 80%).
11. *Populus tremuloides*-*Populus balsamifera*	This forest type is dominated by *Populus tremuloides* (mean density 22 plants/100 m^2, mean BA 2,100 cm^2) and by *Populus balsamifera* (mean density 8 plants/100 m^2, mean BA 1,400 cm^2). It mostly occurs in mesic sites. *Shepherdia canadensis*, *Rosa* spp. and *Potentilla fruticosa* are the most common shrubs. The herb stratum is represented by *Elymus innovatus*.
Coniferous forests	
12. *Picea glauca*-*Elymus innovatus*	Old, dense, mesic forest of white spruce (*Picea glauca*, mean density 32 plants/100 m^2, mean BA 4,800 cm^2). The shrub stratum is represented in decreasing order of importance by *Salix glauca*, *Betula glandulosa* and *Shepherdia canadensis*. The herb layer is represented by *Elymus innovatus* (mean cover 38%), while the cryptogamic stratum is well developed (total mean cover 83%).
13. *Picea glauca*-*Salix* spp.	This forest type occurs in wet, poorly drained and seepage areas. It is recognized by a dense but small size *Picea glauca* (mean density 29 plants/100 m^2, mean BA 3,200 cm^2), and by a dense shrub stratum dominated by *Salix* spp. The herb stratum is mostly represented by sedge species. The total mean cover of the cryptogamic stratum is 92%.

.../continued

14.	*Pinus contorta*-moss	Highly dense forest type dominated exclusively by *Pinus contorta* (mean density 81 stems/100 m^2, mean BA 5,300 cm^2). The shrub stratum is relatively poor with *Shepherdia canadensis* and *Salix glauca* mean densities of 4 plants/100 m^2 and 1 plants/100 m^2 respectively. The low shrub stratum is fairly developed (*Arctostaphylos uva-ursi* mean cover 27%). The herb stratum is represented by *Elymus innovatus* (mean cover 23%) and by *Festuca scabrella* (mean cover 12%). This is the only pine forest where the cryptogamic stratum is significantly present (total mean cover 32%).
15.	*Pinus contorta*-*Shepherdia canadensis*	*Pinus contorta* dominated forest type (mean density 15 stems/100 m^2; mean BA 3,000 cm^2) but without significant pine saplings. Common within the study area in medium to well drained sites. *Picea glauca* (mean density 2 stems/100 m^2), *Populus tremuloides* (mean density 3 stems/100 m^2) and *Populus balsamifera* (mean density 4 stems/100 m^2) also occur. The shrub stratum is dominated by *Shepherdia canadensis* (mean density .25 plants/sqm, mean cover 14%) and in the lower layer by *Arctostaphylos uva-ursi* (mean cover 29%). The herb layer is well developed. *Festuca scabrella* and *Elymus innovatus* are present.
16.	*Pinus contorta*-*Elymus innovatus*	This type is similar to the *Pinus contorta*-*Shepherdia canadensis* type. It differs for occurring in more mesic locations. *Populus balsamifera* is occasionally present in the tree stratum while *Populus tremuloides* regeneration density is relatively high (mean density 12 stems/100 sqm). The shrub stratum is not well developed. The herb stratum presents a dense cover of *Elymus innovatus*.

.../continued

17. *Pinus contorta*-*Picea glauca*	Open forest type characterized by a high density of *Pinus contorta* and *Picea glauca* regeneration (mean density 25 and 24 stems/100 m² respectively). The tree stratum is dominated by *Pinus contorta* (mean density 10 stems/100 m²; mean BA 1,000 cm²). *Picea glauca* is also present (mean density 3 stems/100 m²). The shrub stratum is dominated by *Potentilla fruticosa* (mean density .74 plants/sqm) and *Arctostaphylos uva-ursi* (mean cover 38%). *Betula glandulosa* and *Salix glauca* occasionally occur. *Festuca scabrella* is the most prominent species in the herb stratum. This forest type is common in well drained sites with a relatively recent fire history.

Disturbed Sites

18. Disturbed sites	It includes sites where the vegetation has been disturbed by road-building or other similar human activities. Vegetational features varied from area to area.

CHAPTER THREE

RESOURCE SELECTION

3.1. Introduction

Habitat selection of ungulates is a complex behavioral response to environmental factors whose mechanisms are still little understood. Animals are sensitive to different sensory stimuli from man and therefore identification of environmental factors that are relevant to them is particularly difficult. In this context Moen (1973) introduced the concept of operational environment that describes the sum of habitat components detected by an ungulate that cause some behavioral or physiological response. This concept is similar to the concept of "Umwelt" (subjective space) introduced by Hediger (1951, *in* Leuthold, 1977; Klopfer, 1969) describing "...the sum total of localities and features of significance to the animal (psychologically defined)" (Leuthold, 1977: p. 47).

A number of studies have attempted to define the Umwelt of an animal and generally three basic approaches can be distinguished (Klopfer, 1969). The neurophysiological approach has tried to define sensory ability of the organism under investigation. A second approach is based on the reaction of an organism living in a simplified (artificial) environment to the introduction or variation of single features. The third method of studying the Umwelt of a species has been extensively used by MacArthur (1965 in Klopfer, 1969) and it is based on correlating the presence of species in a community with the characteristics of their environment.

However, it appears that these approaches are not adequate to fully describe habitat selection in ungulates. Eisenberg and Lockhart (1972 in Leuthold, 1977) noted that "...in general, an ungulate species has two major problems to feed itself and to avoid being fed upon". To cope with these two basic requirements, and in order to successfully reproduce, behavioral and non-behavioral characteristics have evolved in an adaptive complex (Leuthold, 1977) of which habitat selection is only an aspect. Therefore, the Umwelt of an ungulate will reflect its size, morphology, food habits, social organization and anti-predator strategy. Further, because animal-environment relationships are a dynamic process and in view of the plasticity of animal behavior (e. g., learning abilities), environment feedbacks play an important role in shaping the relevant habitat of an ungulate species.

Within this conceptual framework any study on habitat selection of an ungulate species is limited. The Umwelt can only be inferred from descriptive behavioral observations and/or from analyzing the response of the species to single environmental factors, knowing little of their interrelationships. In this study habitat selection by bighorn sheep, elk and mule deer was described in relation to specific components of the environment, i. e., vegetation, as classified in Chapter 2, physiographic parameters and weather. In addition, daily activity patterns were described because occupational patterns of animals may vary at different times of day.

3.2. Methods

3.21. Field procedures

From December 1975 to May 1976 data were collected by direct observation of activity, movement and behavior of bighorn sheep, elk and deer. In this regard the study area offered unique opportunities. The presence of several vantage points on the slopes surrounding the valley and on the valley floor allowed to observe animals in forests and to follow their movements throughout the day. This essentially eliminated the impact of the observer on their behavior and reduced visibility bias. In several instances the same herds could be observed for several consecutive days. However, to further offset visibility bias three off-trail routes, proportionally distributed in different forest types, were systematically travelled (Figure 1.1).

Once a group of animals was sighted, date, time, number of individuals, sex and age (if possible) were recorded. Location and movements were marked on a vertical aerial photograph to within 25 m. The site was also described and delineated on a low oblique aerial photograph to within 5 m so that it could be easily located for subsequent description of vegetation. Weather conditions prevailing in the valley at the time of the observation (wind speed and direction, temperature, cloud cover), site descriptors (slope, aspect, snow cover, snow depth and its physical characteristics) and several other factors that might have an impact on species distribution (presence of other species, predators, human activities, etc.) also were recorded (Table 3.1). Emphasis then was placed on behavioral observations for as long as the animals could be observed. From 15 to 20 days were spent each month in the field.

3.22. Analytical techniques

The approach of this study to the analysis of animal behavior and distribution was mainly descriptive. The use by each ungulate species of the eighteen vegetation types previously classified (Chapter 2; Table 2.5) was assessed on the basis of percentage of group sightings. Similarly described was the response of animals to physiographic factors (Table 3.1).

Animal observations were subdivided into two groups; winter observations, from December through March 15th, and

Table 3.1. Potential determinants of animal distribution.

Variable	Unit of Measurement	Methods of Measurement
Physical environment		
1. Slope	Percent	Sunpto level
2. Aspect	Degrees	Compass bearing
3. Elevation	Meters	Altimeter
4. Rockiness	Scores (0-4)	Subjective
5. Distance to cover	Meters	-
6. Heterogeneity	No. of vegetation types within 250 m.	-
Thermal environment		
1. Temperature	°C	Thermographs in representative habitats
2. Wind speed	Meters	Cup anemometer
3. Snow depth	Centimeters	Snow stakes
4. Snow cover	Percent	Subjective
5. Physical charact. of snow	Hardness (g/cm^2)	NRC snow kit
	Density (g/cm^2)	"
	Structure	"

spring observations, from March 16th through May. Seasonal changes in occupational patterns were determined by comparing frequency distributions using contingency table analysis (Nie *et al.*, 1975). For this purpose, descriptors of animal distribution measured in the field as continuous variables (percent, degree, meters) were subdivided in interval-level categories (Table 3.2).

Table 3.2. Interval-level categories used for crosstabulation analysis.

ELEVATION	1 1,500-1,700m	2 1,701-1,900m	3 1,901m-+	
SLOPE	1 0-15%	2 16-28%	3 29-50%	4 51%-+
DISTANCE FROM FOREST COVER	1 5-75m	2 76-150m	3 151-250m	

In contingency table analysis several non-parametric statistics and measures of association are available. Measures of association indicate the strength of relationships between two variables, whereas statistic tests assess the probability that the observed relationship is the result of chance. In this study, measures of association were used to assess whether, for instance, the distribution of a species on the elevational gradient changed with seasons. Because the level of measurement of the variables varied from ordinal (*e. g.*, seasons) to ratio-level (*e. g.*, distance from forest cover) the GAMMA statistic was the most adequate measure of association (Nie et al., 1975). This measure can range from -1 to +1 depending on the direction of relationship between the variables, with 0 value indicating no relationship. The statistical significance of GAMMA value is a standard output of the statistical package. Chi-square test was little used because it gives little information on the strenth of relationships and its value is affected by sample size (Nie et al., 1975; Sokal and Rohlf, 1969: p. 565). To test the significance of differences between two percentages the t-test described by Sokal and Rohlf (1969: p. 607) was used.

Computer contour maps, describing elk distribution before and during a special hunting season, were obtained with the SYMAP package (Dougenik and Sheehan, 1976).

In order to assess the combined effects of wind speed and temperature the windchill index developed by Ames (1974) for cattle and sheep was computed. In this index heat loss (Y) in kcal/day is predicted by the following cubic equation

$$Y = 95.26 + 0.059\ w - 1.1248\ t + 0.0017\ w^2 + 0.0003\ w^3$$

where w = wind speed (mph) and t = temperature (°F).

Shelter-seeking behavior of animals in response to meteorological factors (wind, temperature, cloud cover, windchill index) was analyzed by adopting an approach similar to that of Lewis (1977). Pearson's correlation and multiple step-wise regression programs available in the SPSS computer package were used.

When this study was initiated, slope aspect and snow structure were recorded as potential determinants of animal distribution. However, because slope aspect was found to change little within the study area and snow structure to be insignificant as a determinant of animal distribution on the Ya Ha Tinda Ranch due to its particularly mild climatic conditions, both factors were discarded.

3.3. Results and Discussion

During the field work a total of 471 sightings (group observations), amounting to a total of 24,612 animals, were made (Table 3.3). Due to the small sample size, distribution and occupational patterns of white-tailed deer were not considered in this study.

Table 3.3. Native ungulates observed on the study area. December, 1975 - May, 1976

Species	No. of Animals	No. of Sightings (group observations)
Elk	22,394	239
Bighorn sheep	2,035	151
Mule deer	177	77
White-tailed deer	6	4
TOTAL NO. OF OBSERVATIONS		471

The number of sightings per field day and the average group size of bighorn sheep, elk and mule deer on a monthly basis are shown in Table 3.4.

3.31. Bighorn sheep

3.311. Vegetational environment

As previously noted (section 1.5) three relatively distinct herds of bighorn sheep can be observed on the Ya Ha Tinda Ranch and surroundings. The present study focused on the ecology of the herd ranging on the northern section of the study area. This herd was considered the most likely to interact with the other wild ungulates.

On a cumulative basis (winter-spring) bighorn sheep were mostly associated with open mountain ranges (85 percent of sightings) while only 11 percent of sightings occurred in forest types. This habitat preference generally reflected the overall spatial distribution of the animals over the study area and the location of natural and artificial salt licks on the valley floor (Figure 3.1). In several instances bighorn sheep were observed moving from open grassy slopes through forest cover to salt licks and back. However, on a seasonal basis a definite pattern appeared. Figure 3.2 shows winter and spring distribution of sightings in various vegetation types and activities the majority of the animals was engaged in when first sighted in a vegetation type. During the winter, bighorn sheep were

Table 3.4. Monthly changes in number of group sightings and in average group size of bighorn sheep, elk and mule deer, December 1975-May 1976.

	BIGHORN SHEEP				ELK				MULE DEER			
	n	n/fd	mean	sd	n	n/fd	mean	sd	n	n/fd	mean	sd
DECEMBER	14	1.3	15	13	26	2.5	62	41	-	-	-	-
JANUARY	17	1.6	5	5	11	1.1	9	6	-	-	-	-
FEBRUARY	30	2.0	9	5	27	1.9	141	141	-	-	-	-
MARCH	31	2.2	9	4	46	3.3	197	145	-	-	-	-
APRIL	42	2.3	21	14	72	4.0	105	98	23	1.2	3	1
MAY	17	1.1	11	5	57	3.6	20	29	54	3.3	3	1

n= number of group sightings
mean and sd = average group size and standard deviation
n/fd= number of group sightings per field day

NOTE: Mule deer were not observed in the study area in the winter.

Figure 3.1. Range of bighorn sheep on the Ya Ha Tinda Ranch study area and their routes to natural and artificial salt licks.

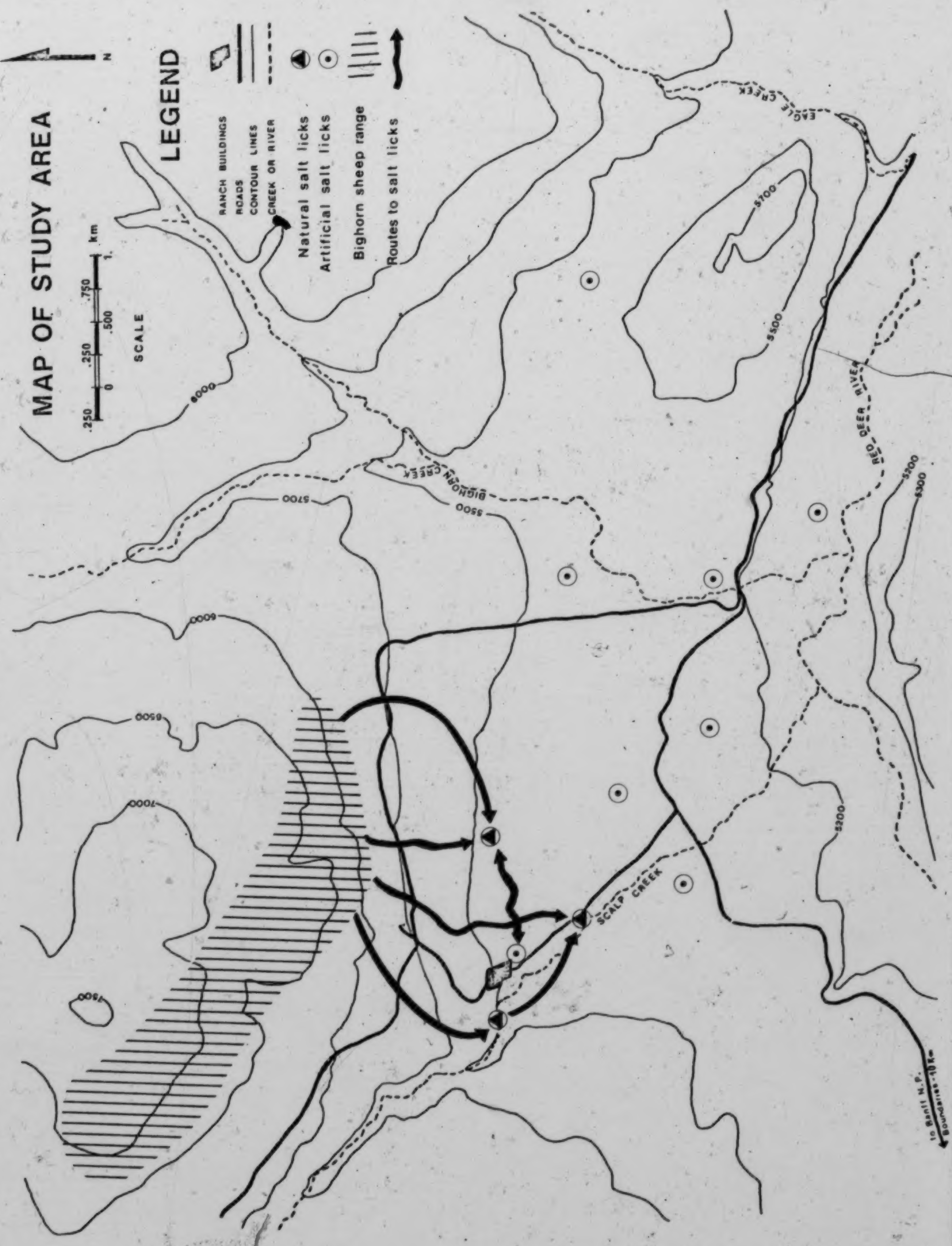

MAP OF STUDY AREA
.250
0
.250
.500
.750
1
km
SCALE
N
LEGEND
RANCH BUILDINGS
ROADS
CONTOUR LINES
CREEK OR RIVER
Natural salt licks
Artificial salt licks
Bighorn sheep range
Routes to salt licks
6000
5700
5500
BIGHORN CREEK
EAGLE CREEK
5700
5500
RED DEER RIVER
5200
5300
6000
6500
7000
7500
SCALP CREEK
5200
To Banff N.P. Boundaries - 10 Km

Figure 3.2. Seasonal distribution of bighorn sheep by vegetation type and principal activities of animals when first sighted.

Vegetation types:

Open mountain ranges:
1. High elevaton ranges
2. Low elevaton ranges

Lower grasslands:
3. Main grassland

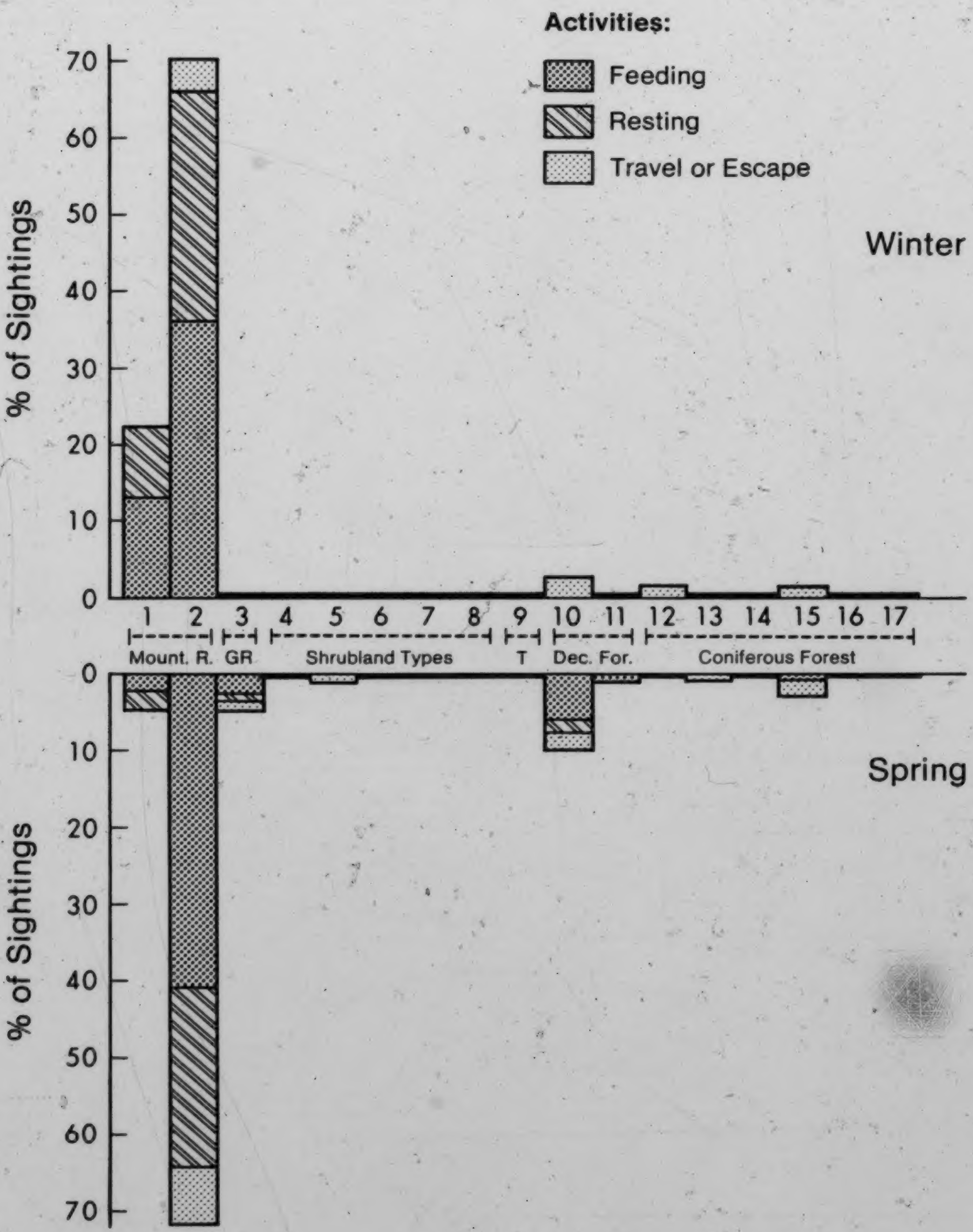
Shrubland types:
4. Dryland shrubs type
5. Tall shrubs type
6. Shrub-swamp type
7. Swamp
8. Forested shrubland

Thicket:
9. *Populus balsamifera*-*Salix* spp.

Deciduous forests:
10. *Populus tremuloides*-*Elymus innovatus*
11. *Populus tremuloides*-*P. balsamifera*

Coniferous forests:
12. *Picea glauca*-*Elymus innovatus*
13. *Picea glauca*-*Salix* spp.
14. *Pinus contorta*-moss
15. *Pinus contorta*-*Shepherdia canadensis*
16. *Pinus contorta*-*Elymus innovatus*
17. *Pinus contorta*-*Picea glauca*

Disturbed sites:
18. Disturbed sites


Activities:
Feeding
Resting
Travel or Escape
Winter
Spring
% of Sightings
% of Sightings
0
10
20
30
40
50
60
70
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Mount. R.
GR
Shrubland Types
T
Dec. For.
Coniferous Forest

mostly observed on open grassy slopes, 70.4 and 22.5 percent of sightings on low and high elevation ranges respectively, while only 5.6 percent were found in forests. In spring, although observations on low elevation grassy ranges remained relatively constant, there was a significant decrease in use of high elevation, rubble mountain slopes (from 22.5 to 5 percent of sightings: t=±3.296 df=148 p<0.001), and a significant increase of occurrence in forests (16.4 percent as compared to 5.6 percent in winter: t=±2.184 df=148 p<0.03). The increase of sightings in forest corresponded to a marked change in activity patterns (Figure 3.2). In winter, bighorn sheep were observed in forest types only when moving to and from salt licks, whereas in spring feeding was recorded in 56 percent of observations in forest. Such a change was particularly evident in the increased use of deciduous forests where feeding and bedding were observed in 66 and 17 percent of cases, respectively. In several instances bighorn sheep were observed slowly drifting, while grazing on grassy slopes, into the adjacent patches of aspen where grazing continued.

Aversion of sheep to forest cover has been emphasized by numerous authors (Oldenmeyer et al., 1971; Shannon et al., 1975). Geist (1971) noted that the animals used forest "...mainly when going to a known location". Brown (1974) reported an actual, though slight, increase in spring occupation of ponderosa pine habitat types by bighorn sheep in northwestern Montana (from 5 to 9 percent). In this study the presence of bighorn sheep in deciduous or coniferous forest could not be accounted for by the presence of predators or human disturbance. In fact forest types were never observed being used as escape terrain. The use of deciduous forest as feeding grounds in spring may be explained as the response of the animals to forage quality and/or availability that, though unexpected (green-up was first observed on grassy slopes), could reflect particular local conditions. However, Shannon et al., (1975) reported little relation in their study area between forage biomass or quality (measured by nitrogen content of palatable species) and bighorn sheep distribution in spring.

Meteorological conditions in part accounted for the use of forests in spring as will be shown in section 3.313.

With regard to bighorn sheep distribution in the vegetational environment, two other parameters were considered, habitat heterogeneity and distance from forest cover. Table 3.5 shows an increased use of more heterogeneous habitats and a higher occurrence of observations closer to forest cover in spring. While the preference for more heterogeneous habitats may simply reflect both the increased use of forest types (e. g., groves of aspen) and the greater proximity to forest cover, the latter is difficult to interpret. Forest cover does not represent an ideal escape terrain, in fact bighorn sheep were always observed reacting to predators (cougars in three

Table 3.5. Seasonal changes in spatial distribution of bighorn sheep as measured by vegetational heterogeneity and distance from forest cover. (Percent of sightings).

	VEGETATIONAL HETEROGENEITY 0	1	2	3	4	DIST. FROM FOREST COV. 1	2	3
WINTER	0	54	35	11	0	37	36	27
SPRING	1	29	46	20	5	52	29	19
	gamma=0.42 p<0.001					gamma=-0.29 p<0.01		

Vegetational heterogeneity: number of vegetation types within 250 m radius.
Distance from forest cover: 1=5-75 m; 2=75-150 m; 3=150-250 m.

cases) by moving succesfully onto the closest steep broken cliff and to hikers or elk hunters by running uphill on open ground further from the source of disturbance.

3.312. Physical environment

In spring, bighorn sheep were observed at lower elevations and on more steep and rocky ground (Table 3.6). Seasonal altitudinal migrations have been reported in numerous studies (Wishart, 1958; Geist, 1971; Shannon *et al.*, 1975) and explained in terms of forage availability (*e. g.*, Wishart, 1958; Geist, 1971) or quality (Hebert, 1973; Shannon *et al.*, 1975). On the Palliser range, Geist (1971) described bighorn sheep winter (November through February) movements after heavy snow falls, from 'rubble' slopes and ridges to the lower grassy slopes and a return to higher ranges once the snow had been swept away by winds. The author also reported a temporary shift in March and April from grassy slopes to steep broken cliffs. This habitat shift was interpreted on the basis of higher forage availability on rocky ground where snow would melt away sooner compared to the adjacent slopes. During the present study snow cover or depth was never found to be a significant factor determining monthly or seasonal distribution of bighorn sheep. In fact, in several instances, different herds could still be found the day after winter snow storms grazing on low and high elevation ranges. The shift to more steep and rocky ground could be

Table 3.6. Spatial distribution of bighorn sheep on the Ya Ha Tinda Ranch. Seasonal changes in elevation, slope and degree of rockiness. (Percent of sightings).

	ELEVATION			SLOPE				ROCKINESS				
	1	2	3	1	2	3	4	0	1	2	3	4
WINTER	4	24	72	27	24	48	1	40	20	22	8	10
SPRING	9	46	45	20	20	54	6	24	32	20	10	14
	gamma=-0.48 p<0.001			gamma=0.21 n.s.				gamma=0.16 n.s.				

Elevation ranges: 1=1,500-1,700 m; 2=1,701-1,900 m; 3=1,901-2,700 m
Slope ranges: 1=0-15%; 2=16-28%; 3=29-50%; 4=51-90%

explained in terms of forage quality. For example, heat retention by rocks during sunny days in late winter and spring may produce warmer microclimatic conditions favorable to an earlier forage green-up and higher nutrient content as compared to adjacent grassy areas. Similarly, the degree of slope as affecting the amount of solar radiation reaching the ground may have a local impact on forage quality. Although these are only hypotheses which were not tested in the field, several authors have noted how bighorn sheep can be highly selective in their foraging strategy (Hebert, 1973; Hudson *et al.*, 1974; Shannon *et al.*, 1975). Spring occupation of more steep and rocky ground could be interpreted also as an anti-predator strategy at a time when animals are in poor condition.

3.313. Weather and thermal environment

In recent years, a bioenergetic approach to understanding animal-habitat relationships has been proposed. The approach considers that undisturbed animals should exibit patterns of activity and habitat selection that result in optimization of the energy budget (Moen, 1973). In this regard the thermal environment can play an important role by affecting animal-environment heat exchanges.

In winter very little use of forest cover by bighorn sheep was observed. Such use was mostly related to movements toward salt licks and could not be accounted for by meteorological variables. Recent physiological studies on the bioenergetics of bighorn sheep showed that animals in winter coat had a lower critical temperature of approximately -30°C in still air and -21°C with wind speed of 18 km/hr (Chappel, 1978). Since such extreme weather conditions were never recorded during field work, this may account for the lack of relationship between thermal conditions and habitat preferences. However, the level of resolution at which this study was conducted also may have played a role in concealing possible relationships. For instance, the use of geomorphic shelter (e. g., small draws) as protection from wind during cold days could not be detected.

However, in spring the use of forest cover during day-light was found to be positively correlated with air temperature and negatively correlated with cloud cover (Table 3.7). This indicates that bighorn sheep sought shelter during hot clear days in nearby forests and tended to make more use of open mountain slopes in relatively cooler or cloudy days. Such shelter-seeking behavior can be explained by the fact that in April and May the animals had not yet shed their winter coat and hence were susceptible to heat stress. The use of cover was not found significantly related to wind speed. However, the combination of air temperature and wind speed in the windchill index resulted in a significant negative correlation. It appears therefore that wind speed alleviates heat stress by increasing heat

Table 3.7. Correlations between use of cover by bighorn sheep and meteorological variables.

	SPRING MR n=16	 MD n=35	 EV n=29
WIND	.35	-.14	.22
AMBIENT TEMP.	.25	.45**	-.13
CLOUD COVER	.30	-.47**	.15
WINDCHILL	-.28	-.44**	.14

MR= Morning (dawn-1/2 hr after sunrise)
MD= Midday
EV= Evening (1/2 hr before sunset-dusk)

**= 0.001<P<0.01

NOTE: Winter correlations were not computed due to the very small number of bighorn sheep observed in forest cover.

dissipation (chilling effect).

Multiple step-wise regression was calculated for midday use of cover in spring and the meteorological variables (Table 3.8). A significant regression was found. The linearly combined effects of cloud cover, air temperature and wind speed explained 25.9 percent of the variance. However, the improvement attributable to wind speed and air temperature (3 and 0.3 percent respectively) was not statistically significant. The regression equation indicates that use of forest cover decreased with increasing cloud cover and wind speed and increased with increasing air temperature. Multiple stepwise regression also was calculated replacing air temperature and wind speed with the windchill index. However, no improvement was achieved since the variance explained by both windchill and cloud cover still amounted to 25.1 percent.

These seasonal differences in shelter-seeking behavior suggest that species adapted to cold environments can be more susceptible to heat than to cold stresses.

3.314. Daily patterns of activity

Although Geist (1971: p. 261) reported Stone's sheep to be more active during the warmest part of the day in winter, no trend in daily pattern of spatial distribution and/or of activity could be detected in the present study.

Table 3.8. Multiple step-wise regression between midday use of cover by bighorn sheep in spring and meteorological variables. Overall F test and summary table.

Use of cover = -.56 -.0004 C -.01 W +.004 T

Multiple R = .509
R square = .259
Adjusted Rsq = .187
Standard error = .399

Analysis of Variance	DF	SS	MS	F
Regression	2	1.733	.578	3.61*
Residual	31	4.952	.160	

Summary table:	Multiple R	R square	Rsq change
Cloud cover (C)	.475	.226	.226**
Wind speed (W)	.506	.256	.030
Ambient temp. (T)	.509	.259	.003

* 0.01<P<0.05
** 0.001<P<0.01

3.315. Sex differential in habitat selection and spatial distribution

Spatial and habitat separation between bighorn sheep rams and ewes on winter ranges has been emphasized by Geist (1971). The author noted that "...large rams and ewes tend to stay on separate wintering areas and if they do winter together may prefer different parts of the same area" (Geist, 1971: p. 71). A similar behavior has also been observed on desert bighorn sheep (State of Utah, 1975; Project No W-65-R-D-23). Recently Geist and Petocz (1977) have attempted to explain male segregation from ewes in terms of maximization of reproductive fitness, i. e., "...males ought not to compete with their own offspring during ontogeny, nor with the prospective mothers of their offspring" (Geist and Petocz, 1977:p. 1803).

Within this conceptual framework, habitat and spatial occupational patterns of bighorn sheep on the Ya Ha Tinda ranch area were analyzed on the basis of herd composition. Group observations were subdivided in three sex-classes termed as follows: "rams", when the group was composed only of adult or subadult males; "ewes", when the group was composed of adult females and subadults, either females or males; "mixed", whenever mature males were present in a "ewe-yearling" class.

Although no difference among sex-classes could be detected in use of vegetation types, a marked contrast was observed in spatial distributions according to the physical environment. Even though both rams and ewes were largely associated with high elevation ranges (Figure 3.3) during the winter months, rams showed a preference for less steep and less rocky ground (Figures 3.4 and 3.5). These results contrast with Geist and Petocz's study (1977) where winter preference by ewes for rocky habitats and by rams for grassy slopes was reported. The authors explained such differential choice as related to the presence of deep snow on slopes. For, rams, being larger and heavier than ewes, could still graze on slopes, whereas ewes had to move onto relatively snow-free cliffs (Geist and Petocz, 1977). The distribution of ewes observed on the Ya Ha Tinda Ranch may indeed reflect different environmental conditions: namely, lack of snow cover on grassy slopes. However, Geist and Petocz (1977) also interpreted the winter preference for grassy slopes by rams in evolutionary terms as "...a behavioral characteristic subject to maturation" (p. 1809). The distribution of rams observed in the present study would not support such speculation since they were found indifferently associated with various degrees of rockiness and in 25 percent of cases on moderately or very steep cliffs (degree of rockiness 3 and 4 respectively, in Figure 3.4).

In spring, the distribution of rams in terms of elevation, percent of slope and degree of rockiness did not change. Ewes instead appeared to have shifted significantly to lower elevations and onto more steep and rocky ground

Figure 3.3. Seasonal distribution of bighorn sheep sex-classes as measured by elevation.

Summary statistics:

Winter
rams vs ewes - chi square=0.03 df=1 n.s.
mixed vs rams - chi square=31.35 df=2 P<0.00001
mixed vs ewes - chi square=13.64 df=2 P<0.001

Spring
rams vs ewes - chi square=20.23 df=2 P<0.00001
mixed vs rams - chi square=21.00 df=2 P<0.00001
mixed vs ewes - chi square=18.39 df=2 P<0.0001

Between seasons
rams vs rams - chi square=2.86 df=2 n.s.
mixed vs mixed - Fisher's exact test. n.s.
ewes vs ewes - chi square=9.60 df=1 P<0.001

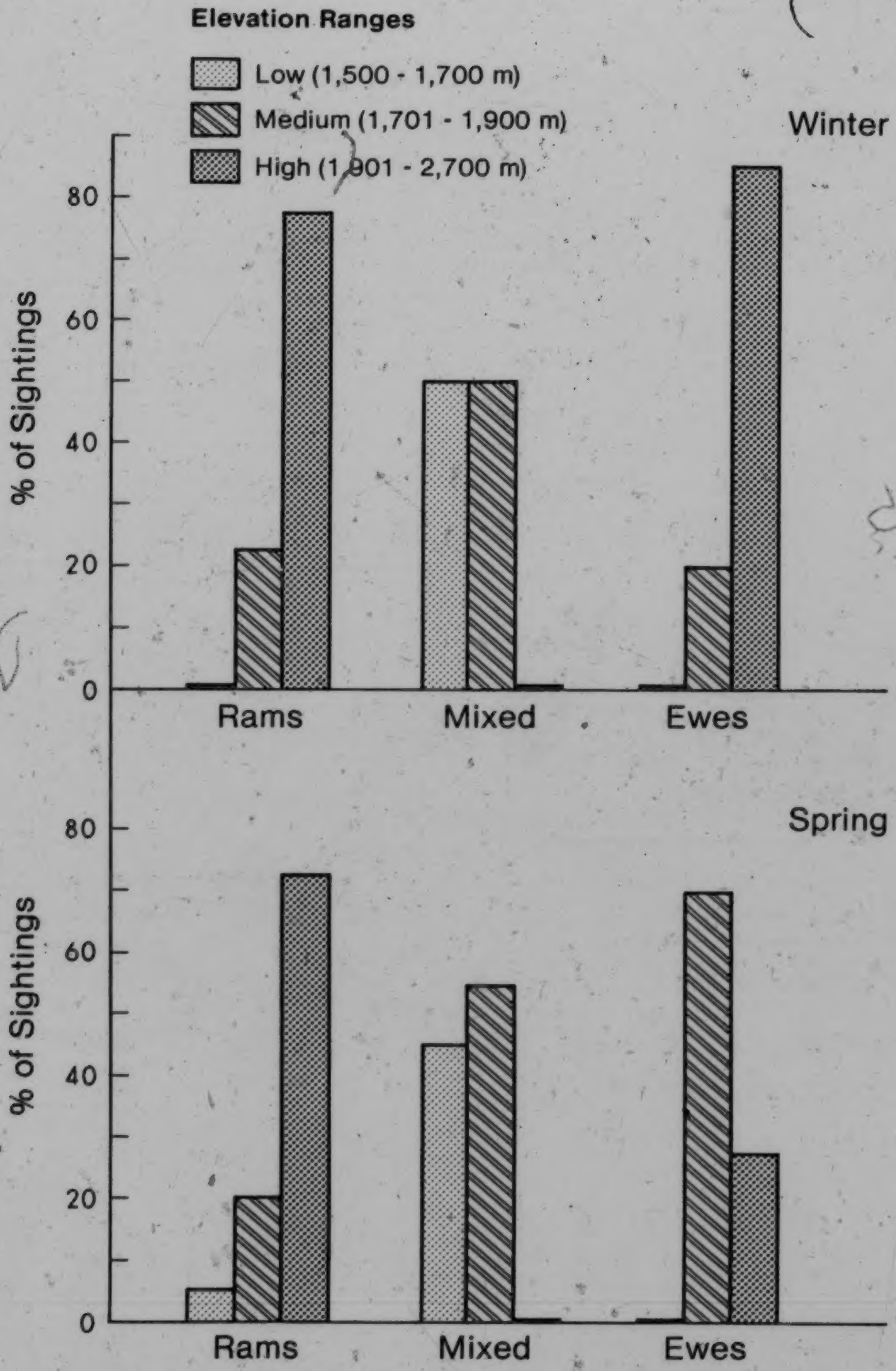

Elevation Ranges
Low (1,500 - 1,700 m)
Medium (1,701 - 1,900 m)
High (1,901 - 2,700 m)
Winter
% of Sightings
80
60
40
20
0
Rams
Mixed
Ewes
Spring
% of Sightings
80
60
40
20
0
Rams
Mixed
Ewes

Figure 3.4. Seasonal distribution of bighorn sheep sex-classes as measured by percent of slope.

Summary statistics:

Winter
rams vs ewes - chi square=27.30 df=3 $P<0.00001$
mixed vs rams - chi square=1.44 df=2 n.s.
mixed vs ewes - chi square=11.44 df=3 $P<0.009$

Spring
rams vs ewes - chi square=0.56 df=3 n.s.
mixed vs rams - chi square=6.71 df=3 n.s.
mixed vs ewes - chi square=8.91 df=3 $P<0.03$

Between seasons
rams vs rams - chi square=5.66 df=3 n.s.
mixed vs mixed - chi square=0.73 df=2 n.s.
ewes vs ewes - chi square=12.45 df=3 $P<0.006$

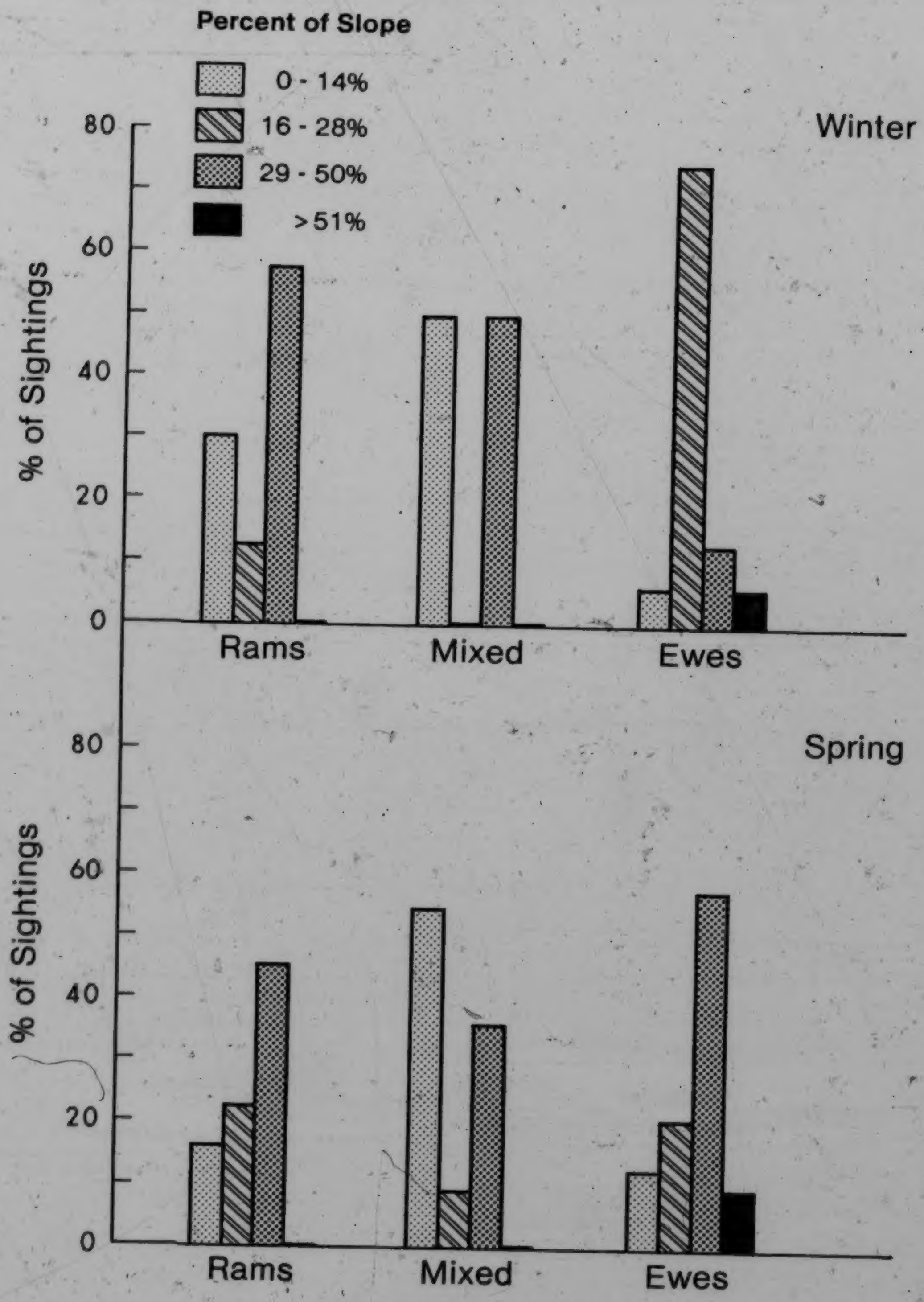

Percent of Slope
0 - 14%
16 - 28%
29 - 50%
>51%
Winter
80
60
40
20
0
% of Sightings
Rams
Mixed
Ewes
Spring
80
60
40
20
0
% of Sightings
Rams
Mixed
Ewes

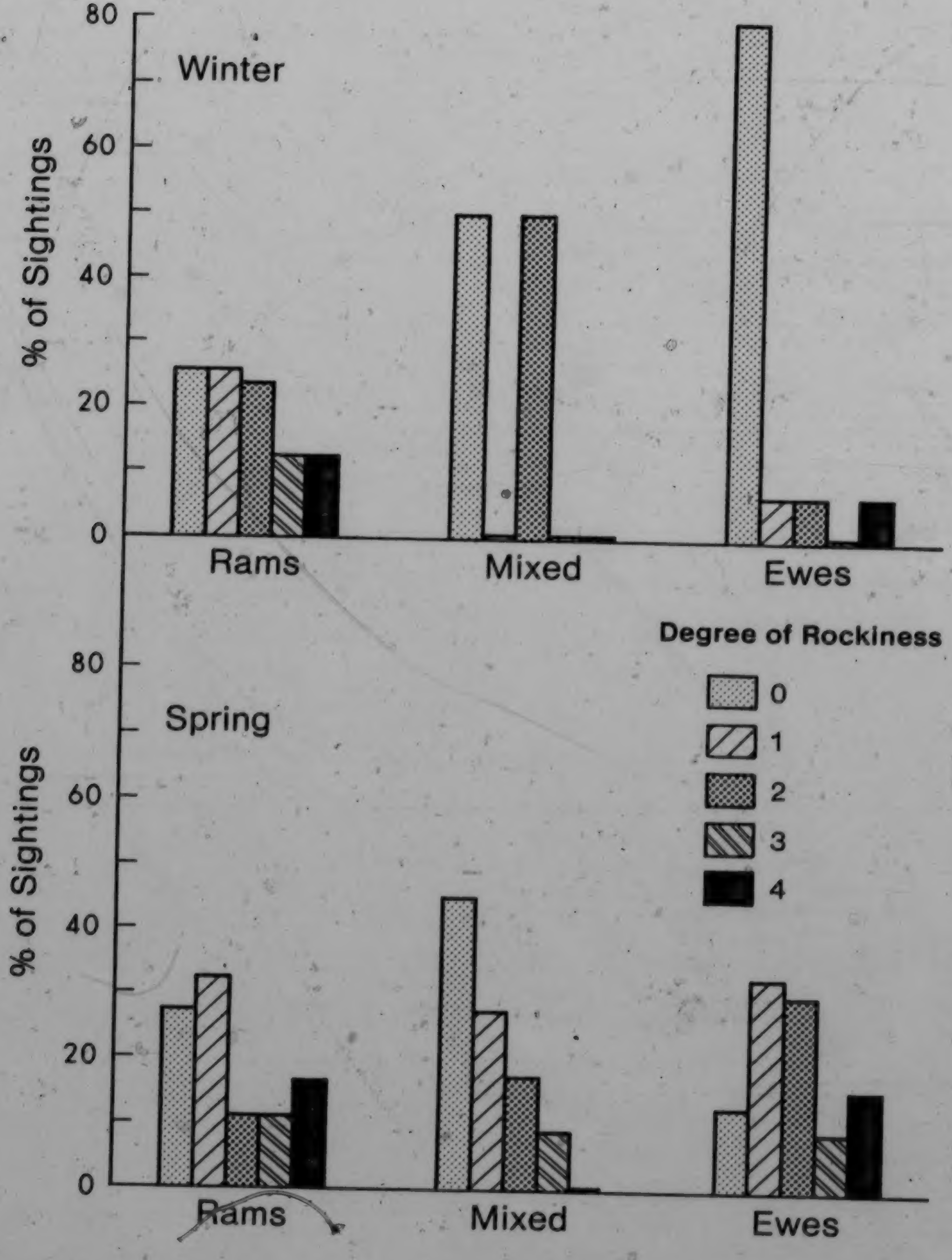
Figure 3.5. Seasonal distribution of bighorn sheep sex-classes as measured by degree of rockiness.

Summary statistics:

Winter
- rams vs ewes - chi square=14.58 df=4 $P<0.005$
- mixed vs rams - chi square=5.43 df=4 n.s.
- mixed vs ewes - chi square=5.56 df=3 n.s.

Spring
- rams vs ewes - chi square=5.29 df=4 n.s.
- mixed vs rams - chi square=3.11 df=4 n.s.
- mixed vs ewes - chi square=6.68 df=4 n.s.

Between seasons
- rams vs rams - chi square=2.62 df=4 n.s.
- mixed vs mixed - chi square=3.53 df=3 n.s.
- ewes vs ewes - chi square=21.65 df=4 $P<0.0002$


80
Winter
% of Sightings
60
40
20
0
Rams
Mixed
Ewes
Degree of Rockiness
0
1
2
3
4
80
Spring
% of Sightings
60
40
20
0
Rams
Mixed
Ewes

(Figures 3.3, 3.4 and 3.5).

With regard to distribution of bighorn sheep as related to distance from forest cover (Table 3.9) and to habitat heterogeneity (Table 3.10), in winter ewes were found more frequently further from forests and in less heterogeneous areas than rams. However, spring distribution showed no difference between sex-classes because in this season ewe groups were observed closer to forests and in more heterogeneous habitats.

The overall seasonal shift by bighorn sheep in their use of the physical environment previously described on a multi-sex basis is mainly attributable to ewes. Greater nutrient requirements for pregnancy, and consequently increased search for high quality forage could account for the shift to lower elevation and to more rocky and steep ground in spring.

The distribution of mixed groups (ewes, yearlings and mature rams) is difficult to interpret. Although no significant seasonal changes could be detected, mixed groups generally were found at lower elevations than both rams and ewes groups, while their distribution in relation to slope, rockiness and distance from forest seems intermediate between rams and ewes. Further, mixed groups preferred higher vegetational heterogeneity than the other social groups (Table 3.10). These differences may be behavioral as related to the presence of mature rams in ewes groups. However, due to the small sample size of mixed groups

Table 3.9. Seasonal distribution of sex-classes of bighorn sheep as related to their distance from forest cover. (Percent of sightings).

	RAMS			MIXED			EWES		
	DIST. FROM FOREST COV.			DIST. FROM FOREST COV.			DIST. FROM FOREST COV.		
	1	2	3	1	2	3	1	2	3
WINTER	46	21	33	33	33	33	13	80	7
SPRING	47	40	13	55	15	30	58	20	22
	gamma=0.18 n.s.			gamma=-0.16 n.s.			gamma=.91 P<0.03		

Distance from forest cover: 1 = 5-75 m; 2 = 75-150 m;
3 = 150-250 m.

Table 3.10. Seasonal distribution of sex-classes of bighorn sheep on the basis of vegetational heterogeneity. (Percent of sightings).

	RAMS					MIXED					EWES				
	VEGETATIONAL HETEROGENEITY					VEGETATIONAL HETEROGENEITY					VEGETATIONAL HETEROGENEITY				
	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
WINTER	0	48	42	10	0	0	17	33	50	0	0	87	13	0	0
SPRING	0	33	47	17	3	9	18	27	36	9	0	24	51	18	5
	gamma=0.29 n.s.					gamma=-0.08 n.s.					gamma=.91 P<0.0001				

Vegetational heterogeneity: number of vegetation types within 250 m radius.

sightings (six in winter, eleven in spring) more specific interpretation is not possible.

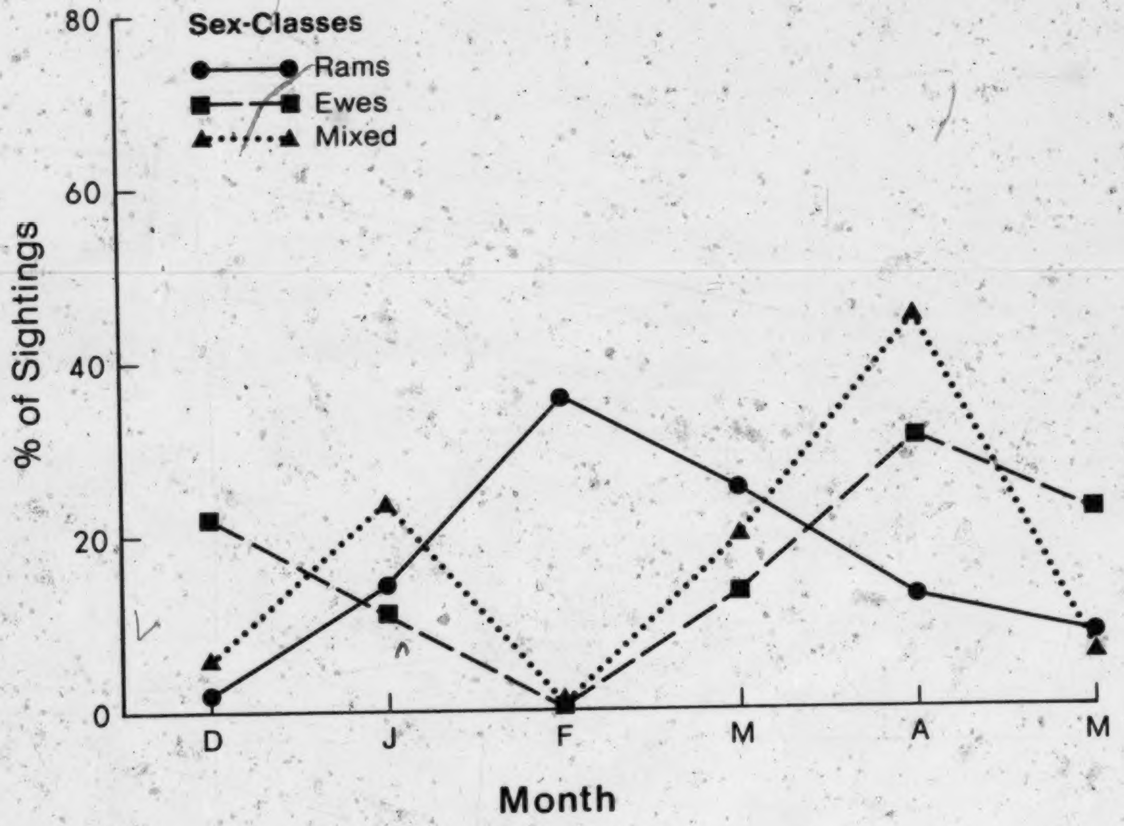
Nevertheless, a sex differential in occupational patterns of bighorn sheep rams and ewes is evident in both seasons. In winter, habitat separation occurred on the basis of rockiness, slope, heterogeneity and distance from forest. In spring elevation was the main factor.

The separation between sexes is further shown by their spatial distribution over their winter range. Ram groups were observed mostly on the east section of the winter range. This section is separated from the west section, where ewes were usually found, by a timbered draw approximately 250 m wide (Figure 3.6) and compared to the west is generally more rocky and steep, with cliffs, talus slopes and patches of vegetation interspersed. The selection of such a section of the whole potential winter range may be seen as related to the small size of ram herds. Therefore, it could be speculated that different patterns of behavior and social organization allow rams to use habitats of higher heterogeneity and thus to be separated from ewes.

Sex differential in behavioral patterns is shown also in Figure 3.7 where monthly sightings of each sex-class are represented. This figure does not indicate avoidance between ewes and rams but only their movements and migrations to and from their main winter range in the study area. In this aspect fluctuations in numbers of ewes and rams are similar tc those described by Geist (1971).

Figure 3.6. Panoramic view of bighorn ewe and ram ranges (on the left and right, respectively) on the Ya Ha Tinda Ranch study area.

Figure 3.7. Group sightings of bighorn sheep sex-classes expressed as monthly percentage of all observations.


Sex-Classes
Rams
Ewes
Mixed
% of Sightings
80
60
40
20
0
D
J
F
M
A
M
Month

According to the author ewes would disperse after the rut and concentrate again in late winter and spring. Rams instead would gradually move to their winter range and then slowly disperse toward intermediate and summer range, possibly following the retreat of snowline (Wishart, 1958).

3.32. Elk

The present study focused on the ecology of cow-calf herds wintering on the Ya Ha Tinda Ranch study area. Adult bulls, single or in small bands, were occasionally observed. Therefore, it appears that sex differential in occupational pattern and spatial distribution is also in effect in the elk population. However, in view of the small number of sightings (n=19) of bull elk within the study area they were not included in the analysis and a comparison among sex-classes could not be conducted.

3.321. Vegetational environment

Figure 3.8 shows the seasonal distribution of elk sightings by vegetation types and activities in which the majority of animals was engaged when first sighted. Shrubland and forest types, because of their relatively uniform use, were further grouped in three broad habitat types as shown on Table 3.11.

Overall (multi-season) elk were found mostly on grassland types (48.8 percent of total number of sightings).

Figure 3.8. Seasonal distribution of elk sightings by vegetation type and principal activities of animals when first sighted.

Vegetation types:

Open mountain ranges:
    1. High elevaton ranges
    2. Low elevaton ranges

Lower grasslands:
    3. Main grassland

Shrubland types:
    4. Dryland shrubs type
    5. Tall shrubs type
    6. Shrub-swamp type
    7. Swamp
    8. Forested shrubland

Thicket:
    9. *Populus balsamifera*-*Salix* spp.

Deciduous forests:
    10. *Populus tremuloides*-*Elymus innovatus*
    11. *Populus tremuloides*-*P. balsamifera*

Coniferous forests:
    12. *Picea glauca*-*Elymus innovatus*
    13. *Picea glauca*-*Salix* spp.
    14. *Pinus contorta*-moss
    15. *Pinus contorta*-*Shepherdia canadensis*
    16. *Pinus contorta*-*Elymus innovatus*
    17. *Pinus contorta*-*Picea glauca*

Disturbed sites:
    18. Disturbed sites

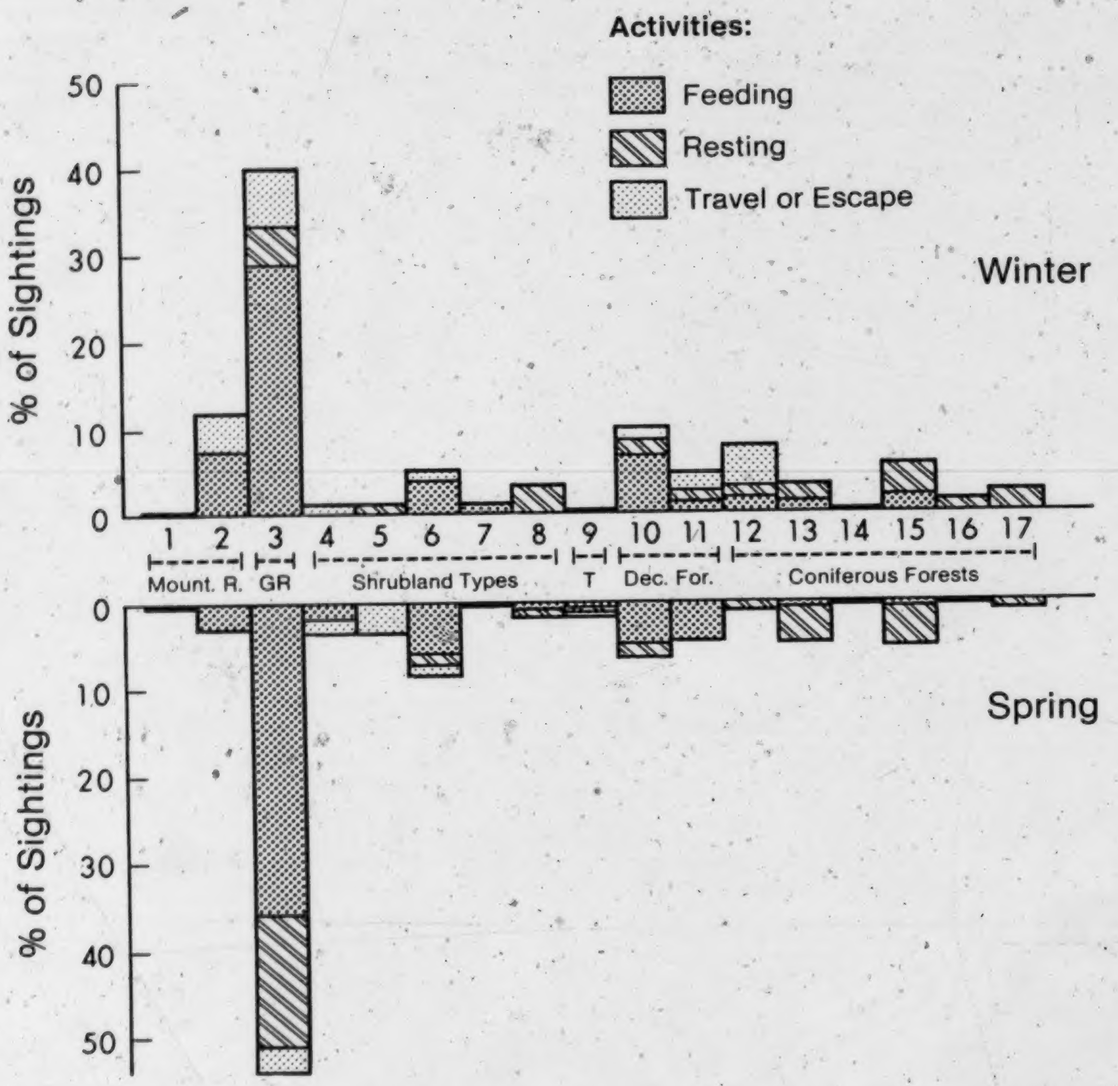

Activities:
Feeding
Resting
Travel or Escape
Winter
Spring
% of Sightings
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Mount. R.
GR
Shrubland Types
T
Dec. For.
Coniferous Forests
% of Sightings
0
10
20
30
40
50

Table 3.11. Seasonal use of major vegetation types by elk. (Percent of sightings).

	WINTER n=85	SPRING n=133	AVERAGE: Dec. 1975-May 1976
MOUNTAIN RANGES	11.8	3.	6.5
GRASSLANDS	40.	54.5	48.8
SHRUBS	12.9	20.5	17.5
DECIDUOUS FORESTS	15.3	8.3	11.1
CONIFEROUS FORESTS	20.	13.6	16.1

Chi square=13.58 df=4 P<0.009

The use of forests (deciduous and coniferous) amounted to 27.2 percent, while occurrences in shrubs and on mountain ranges were 17.5 and 6.5 percent, respectively.

On a seasonal basis a definite trend appeared. In winter elk were observed on grassland types in 40 percent of cases and on mountain ranges in 11.8. Twenty percent of sightings occurred in coniferous forests. Among the five types comprising this latter broad category the Picea-Salix spp. and Pinus contorta-Shepherdia canadensis types appeared the most important, but their significance for the animals markedly differed. The Picea-Salix spp. type was used mostly as travel or escape ground and only in two instances were elk actually observed feeding, whereas the Pinus contorta-Shepherdia canadensis type provided important bedding cover. The use of deciduous forests accounted for 15.3 percent of the total number of sightings and they mostly occurred on the Populus tremuloides-Elymus innovatus type.

Among the shrubland types, the swamp and Picea-Betula types received moderate use during winter, while occurrence in the other types was negligible. The use by elk of open mountain ranges was the result of human harassment during the special hunting season. The approach of hunters from the open grassland forced the animals to move first northward onto bighorn sheep range and then westward into dense cover. This subject will be dealt with more extensively later.

In spring, sightings on grassland types significantly increased to 54.5 percent ($t=\pm2.040$; $P<0.05$), while the use of forests and mountain ranges decreased from 35.3 to 21.9 ($t=\pm2.044$; $P<0.05$), and from 11.8 to 3 percent ($t=\pm2.474$; $P<0.02$) respectively.

The seasonal change in use of vegetation types by elk is particularly relevant when considered in terms of activity patterns (Table 3.12). In spring travel or escape activity was never recorded in forest types nor on open mountain ranges. However, there was a significant increase in elk observed resting on grasslands. Since it is known that elk usually alternate periods of rest with periods of feeding (Craighead *et al.*, 1973; McCullough, 1969; Gates, 1979), the increased use of grassland for bedding indicated an overall spring increase in time spent on this major habitat type.

Decreased use of forests for travel or escape is reflected by the lower number of elk sightings in the *Picea-Salix* spp. and *Populus tremuloides-Elymus innovatus* types (Figure 3.8). Coniferous forests, specifically the *Pinus contorta-Shepherdia canadensis* and *Picea-Elymus* types, were mostly important for providing bedding cover, while both deciduous forest types, *i. e.*, *Populus tremuloides-Elymus innovatus* and *P. tremuloides-P. balsamifera*, for feeding activity. Feeding in deciduous forests occurred at the ground level and very little browsing on sprouts or barking was observed.

Table 3.12. Seasonal use by elk of major vegetation types for feeding, resting and travelling based on initial contact observations. (Percent of sightings).

	MOUN. RANGES			GRASSLAND			SHRUBS			DEC. FORESTS			CON. FORESTS		
	F	R	T	F	R	T	F	R	T	F	R	T	F	R	T
WINTER	70	0	30	73	12	15	45	36	18	61	15	23	35	41	24
SPRING	100	0	0	68	26	6	66	11	23	84	16	0	22	78	0

F=Feeding; R=Resting; T=Travel and escape.

Sightings on shrubland types slightly increased in spring (t=±1.439; n.s.) but their overall use as bedding cover was sharply curtailed. Generally shrublands, due to their location within the study area, were mostly used for travel as will be shown later (see section 3.324). Feeding mainly occurred in the swamp type and should be considered occasional since this type was not selected for feeding but its use was largely associated with movements to and from open grassland.

Elk distribution in terms of vegetational heterogeneity is shown in Table 3.13. No change was observed from winter to spring.

Table 3.13. Seasonal changes in spatial distribution of elk on the Ya Ha Tinda Ranch study area in relation to vegetational heterogeneity. (Percent of sightings).

	VEGETATIONAL HETEROGENEITY					
	0	1	2	3	4	5
WINTER	3.4	18.4	39.1	25.3	8.0	5.7
SPRING	4.7	22.0	36.7	25.3	10.0	1.3

3.322. Physical environment

The selection of vegetation types by elk on the Ya Ha Tinda Ranch study area was not found to be related to physiographic factors. The use of the physical environment generally reflected the main characteristics of the valley floor, that is low elevation, gentle rolling land. Table

3.14 shows elk sightings on the elevational, slope and rockiness gradients. During the winter months the animals were mostly observed at low elevations (1,500-1,700 m) and on level ground. The occurrences at higher elevation and on steep slopes was mostly related to the use of open mountain ranges and appeared attributable to human harassment during the months of January and February (see section 3.325). In spring, elk use of high elevation ranges significantly decreased (t=±2.020; P<0.05). However, observations of elk on steep slopes still occurred. Unfortunately, due to the impact of harassment on the winter distribution of elk, no seasonal comparison could be made.

3.323. Weather and thermal environment

Several authors have indicated the potential impact of meteorological factors on behavior and habitat selection of elk. Responses to winter temperatures (Gaffrey, 1941; Beal, 1974), rain (Harper et al., 1967), wind (Beal, 1974), snow cover and depth (Telfer and Kelsall, 1971; Martinka, 1976; Leege and Hickey, 1977), have been reported. Beal (1974) described a relationship between shelter-seeking behavior in winter and thermal environment. The author concluded that "...elk react to changing ambient temperature and solar and thermal radiation conditions by selecting bedding sites which enhance control of body temperature". Strong relationships between the thermal environment, snow cover and elk behavior have been recorded by Gates (1979).

Table 3.14. Spatial distribution of elk on the Ya Ha Tinda Ranch. Seasonal changes in elevation, slope and degree of rockiness. (Percent of sightings).

	ELEVATION			SLOPE			ROCKINESS				
	1	2	3	1	2	3	0	1	2	3	4
WINTER n=87	69.4	21.2	9.4	72.9	9.4	17.7	90.8	4.6	3.4	1.1	0
SPRING n=133	93.2	4.5	2.3	85.8	3.7	10.5	95.5	3.0	0.8	0.7	0

Elevation ranges: 1=1,500-1,700 m; 2=1,701-1,900 m; 3=1,901-2,700 m.
Slope ranges: 1=0-15%; 2=16-28%; 3=29-50%.

However, various authors have observed behavior to be little affected by weather conditions (Murie, 1951; Leege and Hickey, 1977; McCullough, 1969).

In the closely related European red deer (Cervus elaphus), Staines (1976) described shelter-seeking behavior in response to an increasing windchill factor. But the author noted that the animals found protection from wind "...by lying on lee slopes, in long vegetation, on dry ground and in places with small amounts of geomorphic shelter..." and that "...they sought very sheltered places only during blizzards". With regard to warm weather, red deer were found to be susceptible to heat stress (Staines, 1970 in Staines, 1974).

In the present study, snow was not found to be a factor determining elk distribution during the winter of 1975-76. For most of the season the large open grassland was kept snow-free by westerly winds while snow depth in forest cover never exceeded 35 cm (14 inches) at any one time. Such snow depth was below the value at which elk would respond by moving to other areas (Leege and Hickey, 1977).

No relationship was observed between habitat selection and the thermal environment as measured by ambient temperature, wind speed and cloud cover. Table 3.15 shows correlation coefficients between use of cover and meteorological variables.

Table 3.15. Seasonal correlations between use of cover by elk and meteorological variables.

	WINTER			SPRING		
	MR n=17	MD n=25	EV n=26	MR n=26	MD n=45	EV n=78
WIND	-.009	-.16	-.19	-.23	-.08	-.10
AMBIENT TEMP.	-.12	.003	-.22	.18	-.28	.09
CLOUD COVER	.009	-.12	.003	.05	.23	.04
WINDCHILL	.12	-.003	.18	-.18	.27	-.09

MR= Morning (dawn-1/2 hr after sunrise)
MD= Midday
EV= Evening (1/2 hr before sunset-dusk)

Although a winter trend in the use of shelter in the mornings and evenings during cold weather is apparent, the lack of significant correlations is not surprising. Beal (1974) noted that shelter-seeking was a behavioral response to air temperatures below -18°C (0°F) and wind speed of 24 km per hour. During the winter of 1975-76 these two values were never concurrently recorded. In addition, similar to the behavior described by Staines (1976) in red deer, elk could easily find protection from wind using geomorphic shelter in the rolling grassland and through behavioral means (e. g., lying). Trends during daylight hours are hard to interpret. On the basis of the correlations elk would seek shelter with decreasing wind speed and cloud cover. This behavior cannot be explained in terms of thermal amelioration. It is suggested therefore that other factors such as disturbance played a role in determining use of cover by elk during day time (see sections 3.512d and e) and thus concealed the impact of thermal conditions.

In spring, whereas bighorn sheep and mule deer were affected by heat stress and sought shelter during hot clear days elk did not show a significant response. This difference is difficult to explain. Correlation coefficients (Table 3.15) for mornings and evenings show a trend in the use of shelter during warm weather (i. e., low wind speed, high air temperature and low windchill). However, the values obtained during daylight hours are not easily interpreted. The trend indicates use of cover with low temperatures ($r=.277$, two-tailed test: $P<0.06$) and high cloud cover. In other words elk in spring, when still in their winter coat, would be found more frequently in the open during warm, clear days. According to the theory, in such thermal conditions the animals would be susceptible to heat stress (Staines, 1970, in Staines, 1974) and seek shelter, as observed in bighorn sheep and mule deer during the present study. A possible explanation to these results can be found by observing the range of spring ambient temperatures used for correlation analysis. Whereas winter and spring ranges of wind speed, windchill and cloud cover were similar for the three species, spring temperature ranges varied significantly. Bighorn sheep and mule deer were observed at temperatures varying between -6° and +20°C (mean=+4°C) and -4° and +21°C (mean=+8°C), elk sightings occurred at temperatures varying between -7° and +14°C (mean=3°C). Therefore the lack of a relationship may be because the air temperatures considered in the analysis never reached sufficiently high values to cause heat stress.

The differences in spring air temperatures among the three ungulate species in part reflects their general habitat preference (e. g., open mountain slopes, valley floor, etc.). However, it may indicate also a bias in elk sightings in late spring, at the time of calving season, when the use of forest by small herds and isolated cows during warm days may have been undetected.

3.324. Daily patterns of activity

The selection of vegetation types and spatial distribution by elk appeared to be strongly related to time of day (Figure 3.9) and to the distance of vegetation types from roads (Figure 3.10).

In general, the elk population showed a remarkably predictable activity pattern. This consisted in winter of early morning movements from open grassland, through shrubland, into deciduous and coniferous forests (furthest from roads) where the animals remained during the day. The frequency histogram in Figure 3.10 reflects such winter movements as well as the location of each habitat type in relation to roads. Later in the day, a reverse movement toward the open grassland occurred. The amount of time the elk spent in shrubland, while moving toward the open in evening, appeared related to traffic activity taking place on the road. Once on the grassland, grazing took place within 100-200 m of cover (Figure 3.11 a,b,c). With darkness, the elk moved closer to the main road making better use of the potentially available range.

In spring the elk moved out from cover at the same time of day as in winter. However, after a period of grazing they bedded down in the same spot, close to cover, and movements toward the centre of the open grassland did not occur until darkness. Thus, elk spent more time close to shrubland, and less time in central grassland near roads, in spring as compared to winter. In both seasons the

Figure 3.9. Selection of major vegetation types by elk in winter in relation to time of day.

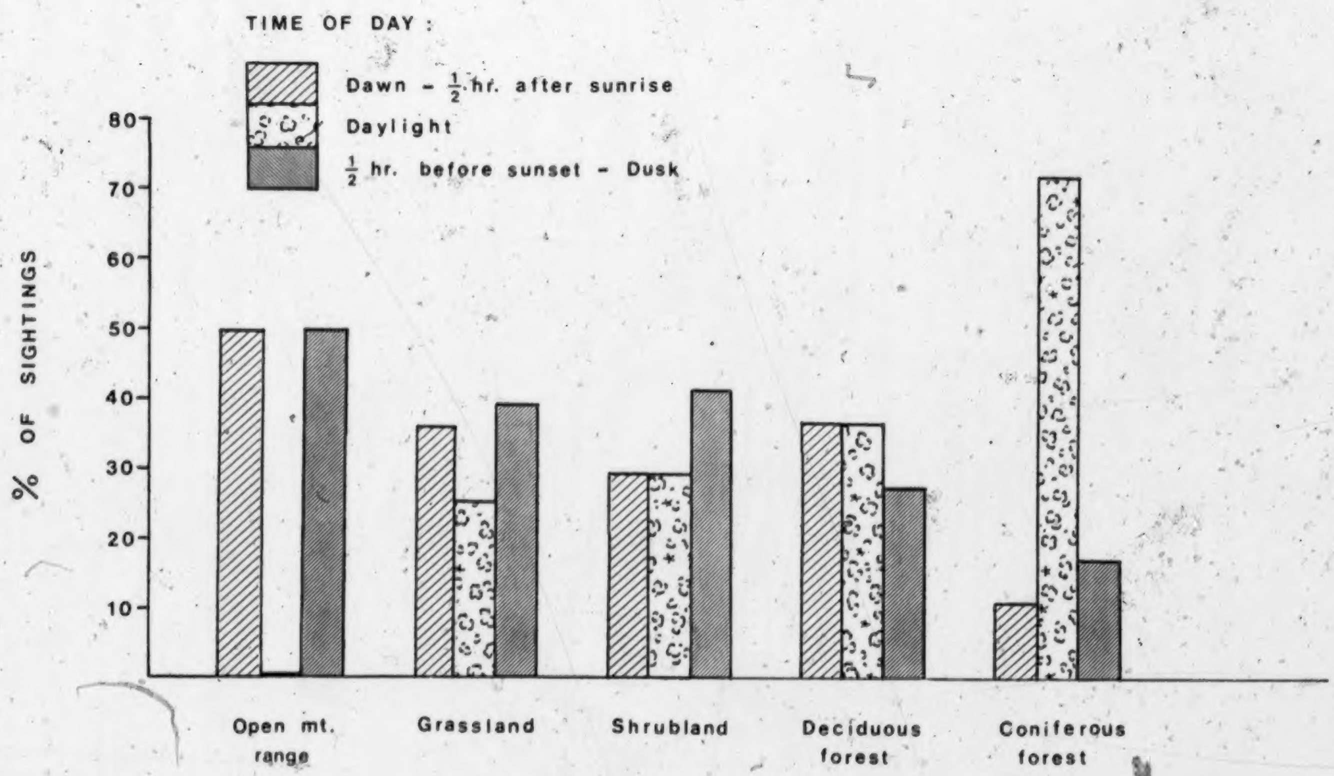

TIME OF DAY :
Dawn - $\frac{1}{2}$ hr. after sunrise
Daylight
$\frac{1}{2}$ hr. before sunset - Dusk
% OF SIGHTINGS
80
70
60
50
40
30
20
10
Open mt. range
Grassland
Shrubland
Deciduous forest
Coniferous forest

Figure 3.10. Selection of major vegetation types by elk in winter in relation to distance from road.

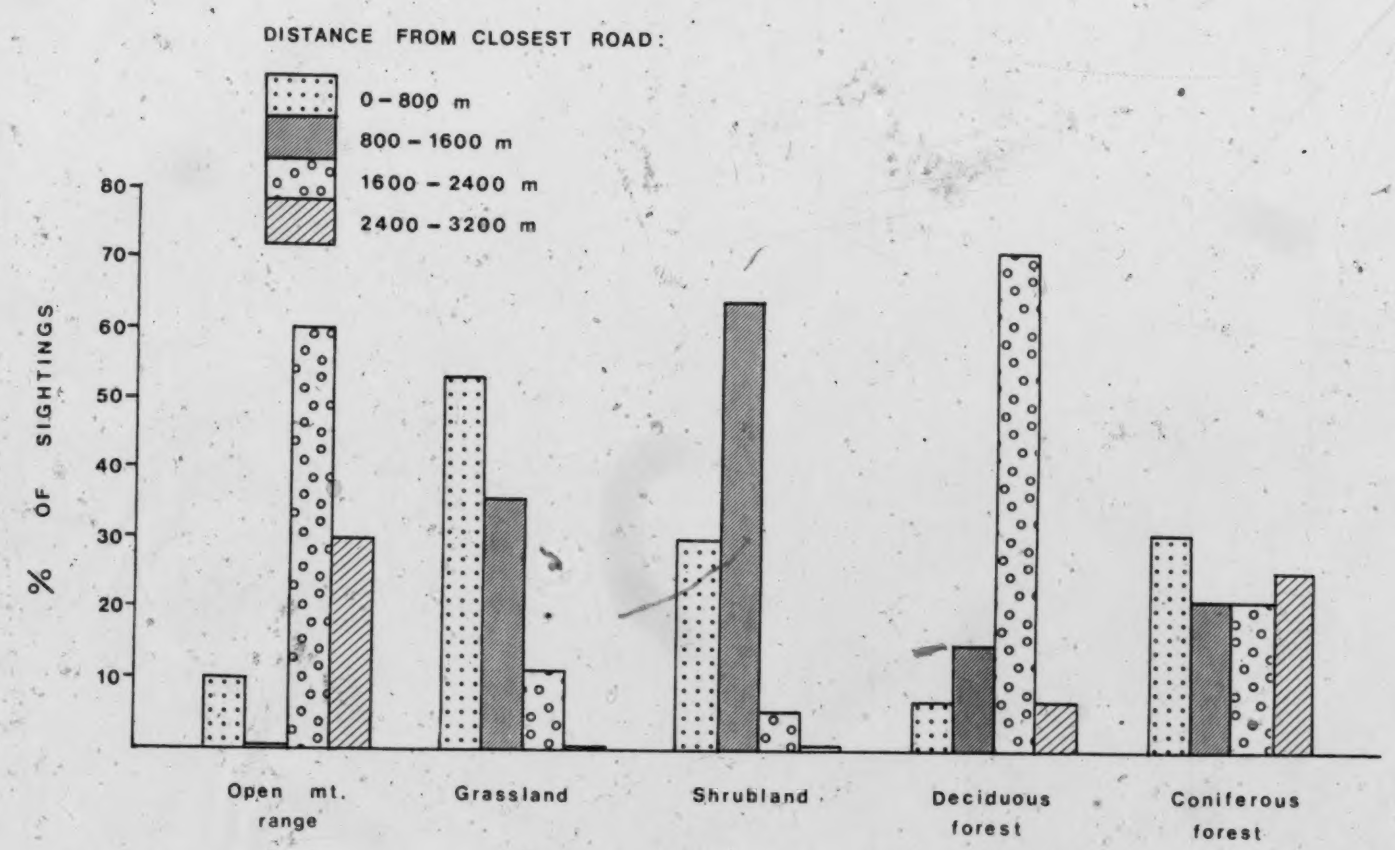

DISTANCE FROM CLOSEST ROAD:
0 – 800 m
800 – 1600 m
1600 – 2400 m
2400 – 3200 m
% OF SIGHTINGS
80
70
60
50
40
30
20
10
Open mt. range
Grassland
Shrubland
Deciduous forest
Coniferous forest

Figure 3.11 a,b,c. Evening movements of elk from cover toward the open grassland in winter.

a.

b.

c.

selection of vegetation types differed on the basis of the characteristics of the site. For instance, the use of the large open grassland, intersected by the road system and in full sight of it, was restricted to the period between evening and early morning, but elk were observed during the day on patches of grassland out of sight of roads.

The daily activity pattern was consistent throughout the study period but it was observed only west of Bighorn Creek (Figure 1.1), near the road system. East of the creek the same population of elk could be observed in the open throughout the day. A road also was located in this vicinity, but was 2 km from the elk range and at 100 m lower elevation.

It is difficult to explain the difference in elk behavior between the two sections of the study area in terms of immediate disturbance responses. At the time of this study, traffic activity west of the creek, though unpredictable, was not heavy and it was mostly limited to weekends. Also, traffic activity related to the operation of the horse ranch was negligible. However, from 1969 to 1975, with the exception of 1972, a special hunting season (either sex) was held in winter. The elk population was subjected to heavy hunting pressure (see Marty, 1978: pp. 240-248) that resulted in an average harvest of 112 animals per season. Therefore, it is suggested that the extremely wary behavior of this population may be related to that experience. East of Bighorn Creek, the animals would feel more secure as compared to western sections of the study area. Similar secretive habits of red deer in response to hunting pressure were described by Batcheler (1968). The author noted that "the secretive habits were retained for at least two years after cessation of hunting". Douglas (1971) reported that red deer and chamois (_Rupicapra rupicapra_) in New Zealand returned to diurnal feeding in open grassland two years after intensive hunting had ceased. A shift toward nocturnal habits by red deer in response to disturbance has been described by Ueckerman _et al_. (1975).

Daily movements of elk from timber onto open grassland and vice versa are well known in the literature. Generally this behavior is considered characteristic of the species and therefore no particular attempt is made to document or explain it. Indeed there are many seasonal and environmental factors that may determine elk use of cover during day-light hours, _e. g._, insect avoidance or thermal-amelioration in cold environments. The results of this study suggest that learned avoidance of human activities may play the most important role in determining use of cover by hunted elk populations when other environmental conditions are met. Such learned behavior also could prevent elk from optimizing spatial distribution and habitat selection.

3.325. Impact of harassment and hunting on elk distribution

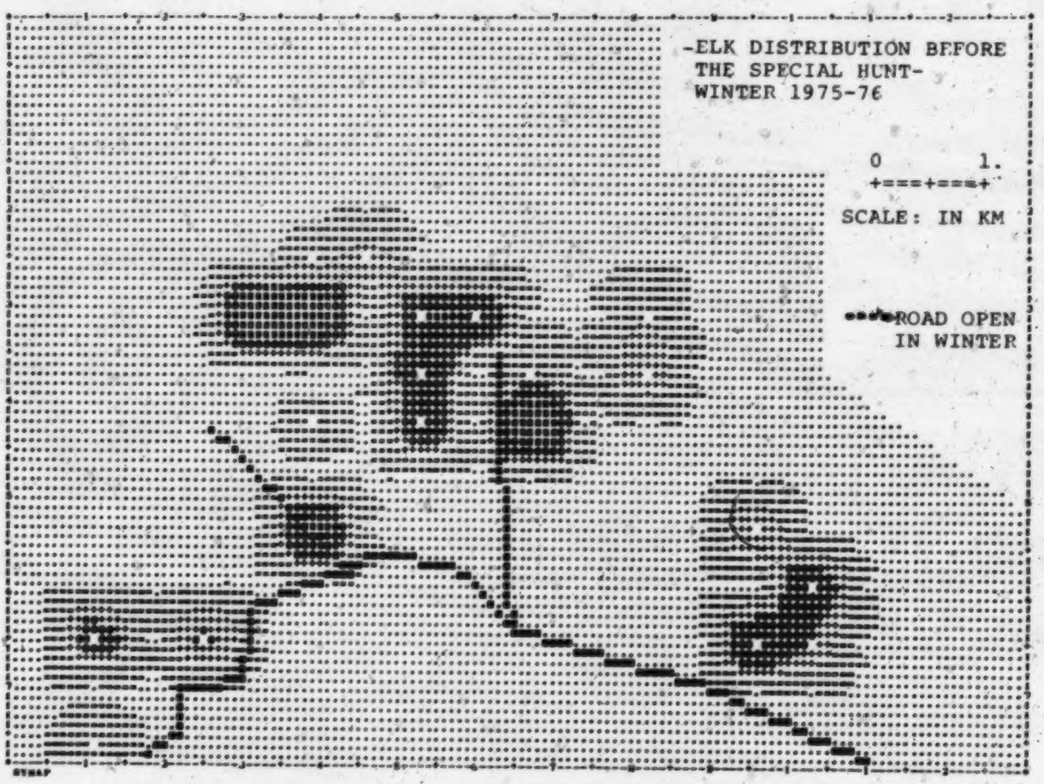
One of the first descriptions available on the effects of harassment on the Rocky Mountain elk is that of Altmann (1956). The author concluded: "...in a situation of persecution, which was one of severe stress and strain, the elk reacted by evasion and rutting activity was curtailed, or perhaps even supressed...". But until the early 1970's, little was reported on the harassment factor as it may affect habitat selection (Lyon 1971, Ream 1972).

Recently, however, several authors have dealt with the impact of recreational and industrial activities and traffic on elk behavior (Ward _et al_. 1973; Bohne, 1974; Rost, 1975). Significant reductions in elk use of different habitat types, caused by the presence of roads and associated activities, have been described by Perry and Overly (1976), Hershey and Leege (1976), and others.

In this study the impact of a special hunting season on the distribution of the elk population was investigated. The special season, restricted to males, was held during the first two weekends of January and February. A total of 200 licences were issued, 50 each weekend.

Figures 3.12 and 3.13 represent contour maps of elk density and distribution prior to and during the hunting season, respectively. Increasingly darker areas symbolize increasing elk density expressed as number of individuals per .25 sq km.

Figure 3.12. Contour map of elk distribution before the special hunting season. Increasingly darker areas symbolize increasing elk density expressed as number of individuals per .25 sq. km.

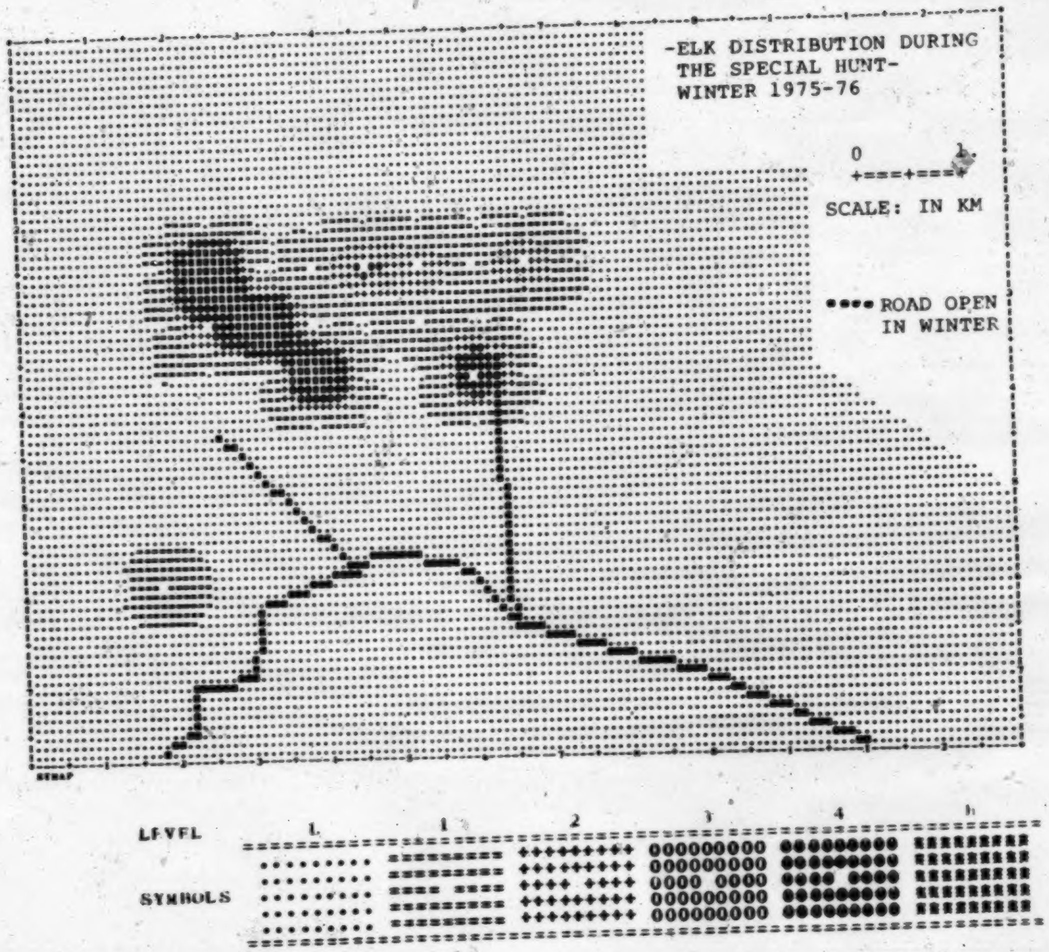

-ELK DISTRIBUTION BEFORE
THE SPECIAL HUNT-
WINTER 1975-76
0 1.
+===+===+
SCALE: IN KM
ROAD OPEN
IN WINTER
SYMAP

```
LEVEL           L          1          2          3          4          H
           ==================================================================
             .........  =========  +++++++++  000000000  ●●●●●●●●●  ■■■■■■■■■
             .........  =========  +++++++++  000000000  ●●●●●●●●●  ■■■■■■■■■
SYMBOLS      .........  ==== ====  ++++ ++++  0000 0000  ●●●● ●●●●  ■■■■■■■■■
             .........  =========  +++++++++  000000000  ●●●●●●●●●  ■■■■■■■■■
             .........  =========  +++++++++  000000000  ●●●●●●●●●  ■■■■■■■■■
           ==================================================================


DATA VALUE EXTREMES ARE          0.0        220.00


ABSOLUTE VALUE RANGE APPLYING TO EACH LEVEL
      ('MAXIMUM' INCLUDED IN HIGHEST LEVEL ONLY)
                                                                      ABOVE
 MINIMUM       BELOW       1.00      26.00      51.00      76.00     101.00
 MAXIMUM        1.00      26.00      51.00      76.00     101.00
```

Figure 3.13. Contour map of elk distribution during the special hunting season. Increasingly darker areas symbolize increasing elk density expressed as number of individuals per .25 sq. km.


-ELK DISTRIBUTION DURING
THE SPECIAL HUNT-
WINTER 1975-76
0
1
SCALE: IN KM
ROAD OPEN
IN WINTER
LEVEL
1
1
2
3
4
5
SYMBOLS

```
DATA VALUE EXTREMES ARE          0.0          200.00


ABSOLUTE VALUE RANGE APPLYING TO EACH LEVEL
     ('MAXIMUM' INCLUDED IN HIGHEST LEVEL ONLY)
                                                                    ABOVE
  MINIMUM       BELOW        1.00        26.00       51.00       76.00      101.00
  MAXIMUM        1.00       26.00        51.00       76.00      101.00
```

Whereas prior to the hunting season elk were widely distributed on the valley floor (Figure 3.12), with a pattern that reflected movements and behavior previously described, their distribution changed significantly during the hunting season. A shift north to higher elevation was observed, while the whole open grassland intersected by the road system was abandoned (Figure 3.13).

The impact of the hunting season is reflected also in the low number of sightings, indicating a general movement out of the study area, and in smaller herd sizes during the months of January and February (Table 3.3).

Elk distribution in relation to the distance from roads prior to, during (January 1-February 15) and after the hunting season, and in March, is shown in Figure 3.14. The frequency histogram shows a shift to the right during the hunting period (i.e., an increased number of observations further from the road during the hunting period), and a gradual shift to the left afterwards, reflecting restoration of the original distribution pattern.

Movement of elk to higher elevations during the hunting season is illustrated in Figure 3.15. The altered pattern of elk distribution caused a significant change in the use of major vegetational types (Figure 3.16). During the hunting season elk displacement from the main grassland on the valley floor resulted in a 70 percent decrease in grassland use, a 65 percent increase in the use of open mountain ranges and a 20 percent increase in the overall use

Figure 3.14. Distribution of elk before, during and after the special hunting season and in March, in relation to distance from roads.

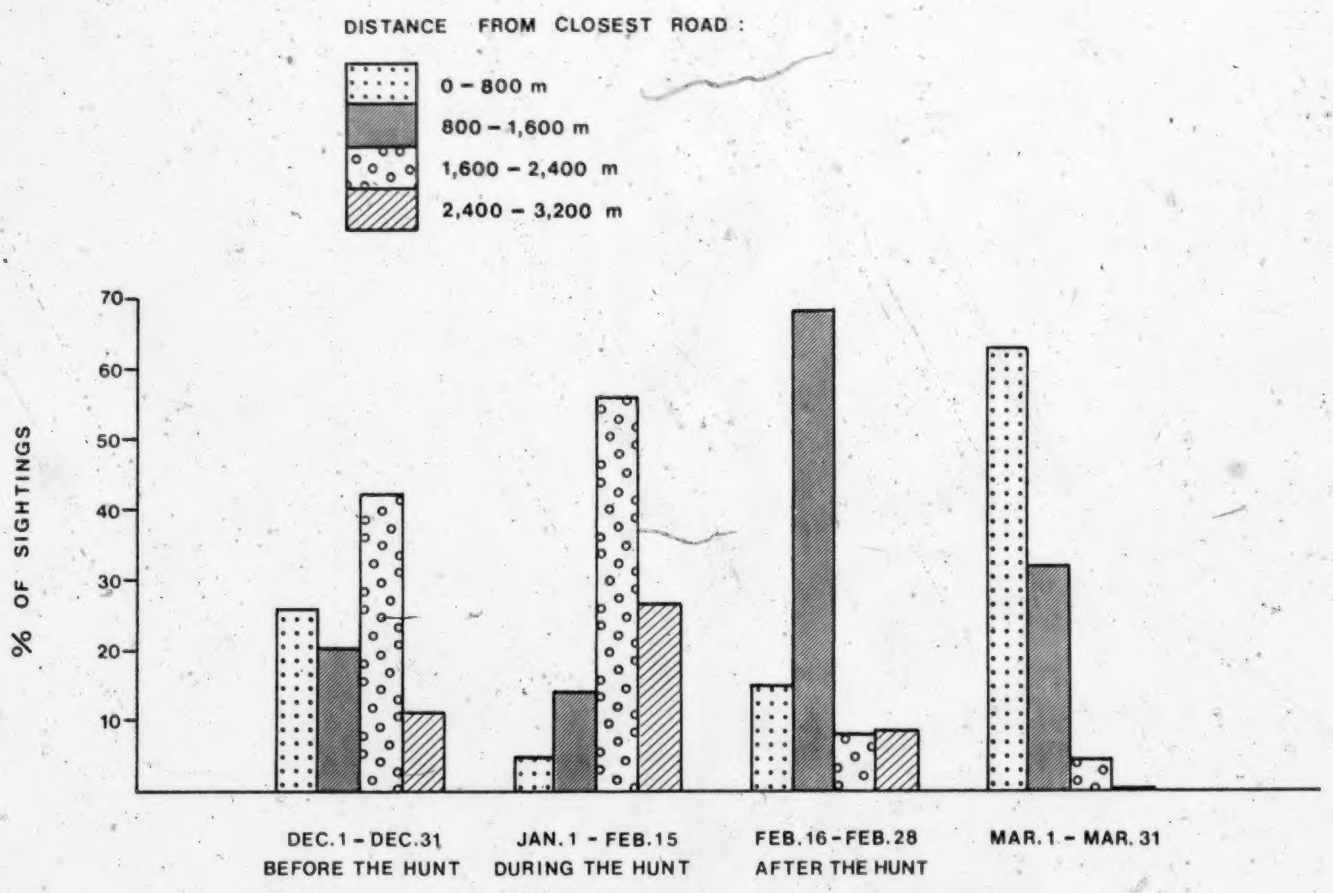

DISTANCE FROM CLOSEST ROAD :
0 – 800 m
800 – 1,600 m
1,600 – 2,400 m
2,400 – 3,200 m
% OF SIGHTINGS
70
60
50
40
30
20
10
DEC.1 - DEC.31
BEFORE THE HUNT
JAN.1 - FEB.15
DURING THE HUNT
FEB.16 - FEB.28
AFTER THE HUNT
MAR.1 - MAR.31

Figure 3.15. Elevational distribution of elk sightings before, during and after the special hunting season.

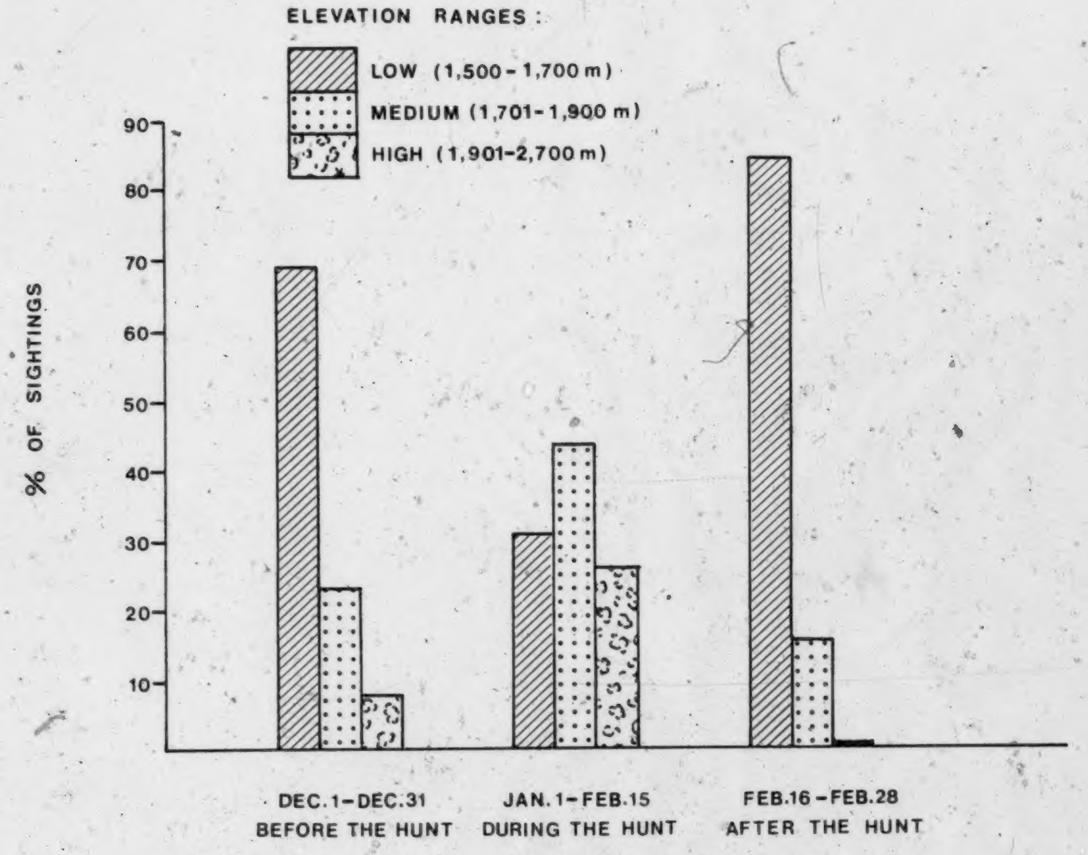
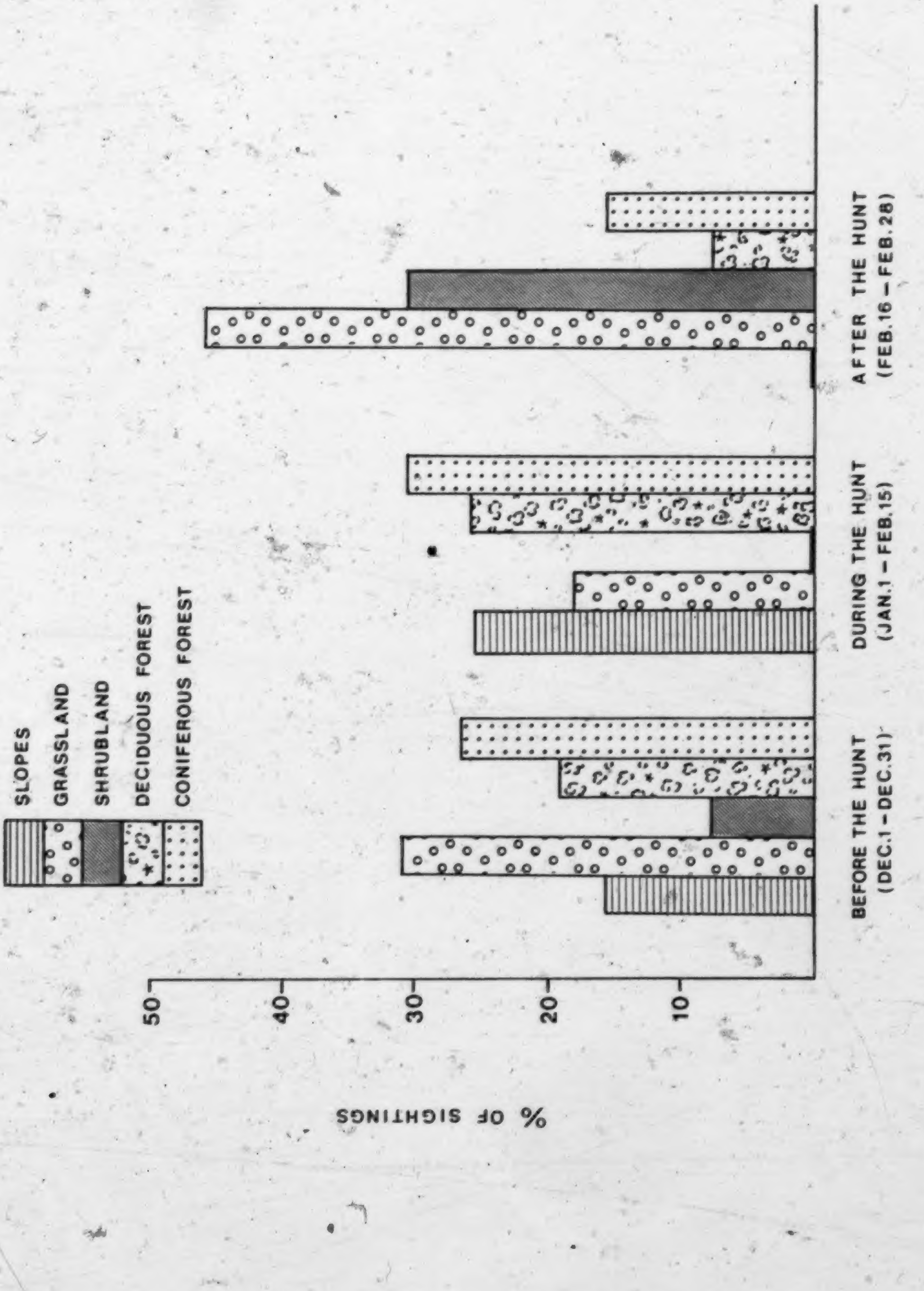

ELEVATION RANGES:
LOW (1,500-1,700 m)
MEDIUM (1,701-1,900 m)
HIGH (1,901-2,700 m)
% OF SIGHTINGS
90
80
70
60
50
40
30
20
10
DEC.1-DEC.31
BEFORE THE HUNT
JAN.1-FEB.15
DURING THE HUNT
FEB.16-FEB.28
AFTER THE HUNT

Figure 3.16. Use by elk of major vegetation types before, during and after the special hunting season.


SLOPES
GRASSLAND
SHRUBLAND
DECIDUOUS FOREST
CONIFEROUS FOREST
% OF SIGHTINGS
50
40
30
20
10
BEFORE THE HUNT
(DEC.1 – DEC.31)
DURING THE HUNT
(JAN.1 – FEB.15)
AFTER THE HUNT
(FEB.16 – FEB.28)

of forested areas. After the hunting season elk were not observed on the open slopes, while there was a 154 percent increase in use of grassland. These results differ from Irwin and Peek's (1978) description of elk displacement to areas of similar but more extensive habitat and are clearly an indication of a different regional physiography.

Differences among the three periods in use of shrubland and open mountain ranges illustrated in Figure 3.16 require explanation. In December, the elk were still moving from alpine summer ranges down to the valley floor. This may explain observed use of this habitat in December (Figure 3.16) as well as the small percentage of elk observations at high elevation (Figure 3.15) and further from roads (Figure 3.14). It is therefore suggested that harassment associated with hunting activity on the valley floor reversed the downward migratory movement.

The high use of shrubland after the hunt (Figure 3.16) reflects activity patterns of the elk population described earlier, that is, movements to and from open grassland through shrubland. It also indicates that elk may use certain vegetation types (in this study shrubland) because of their proximity to preferred areas, rather than in response to vegetation structure or to other habitat attributes per se.

3.33. Mule deer

Ecology and behavior of mule deer on the Ya Ha Tinda Ranch study area are little understood. Mule deer usually are not present in the area during the winter months (December-March) and it is not known whether in this season they are scattered in the surrounding areas or they have moved farther east. Therefore, this study deals only with their distribution and occupational patterns in spring.

During the study, mostly does and yearlings were observed. This may indicate a difference in spatial distribution between mule deer does and bucks similar to that described in bighorn sheep and postulated for the elk population. However, a sex differential in mule deer ecology could not be directly demonstrated because of the small number of observations of mule deer bucks.

3.331. Vegetational environment

Sightings of mule deer by vegetation types and activities in which the majority of the animals was engaged when first sighted are represented in Figure 3.17. Sightings were further grouped in six broad vegetation types as shown in Table 3.16.

Mule deer generally were uniformly distributed among five-six vegetation types (Figure 3.17). However, on a broad basis deciduous forests were the most used (32.5 percent of sightings), coniferous forests and open

Figure 3.17. Distribution of mule deer sightings by vegetation type and principal activities of animals when first sighted.

Vegetation types:

Open mountain ranges:
  1. High elevaton ranges
  2. Low elevaton ranges

Lower grasslands:
  3. Main grassland

Shrubland types:
  4. Dryland shrubs type
  5. Tall shrubs type
  6. Shrub-swamp type
  7. Swamp
  8. Forested shrubland

Thicket:
  9. *Populus balsamifera*-*Salix* spp.

Deciduous forests:
  10. *Populus tremuloides*-*Elymus innovatus*
  11. *Populus tremuloides*-*P. balsamifera*

Coniferous forests:
  12. *Picea glauca*-*Elymus innovatus*
  13. *Picea glauca*-*Salix* spp.
  14. *Pinus contorta*-moss
  15. *Pinus contorta*-*Shepherdia canadensis*
  16. *Pinus contorta*-*Elymus innovatus*
  17. *Pinus contorta*-*Picea glauca*

Disturbed sites:
  18. Disturbed sites

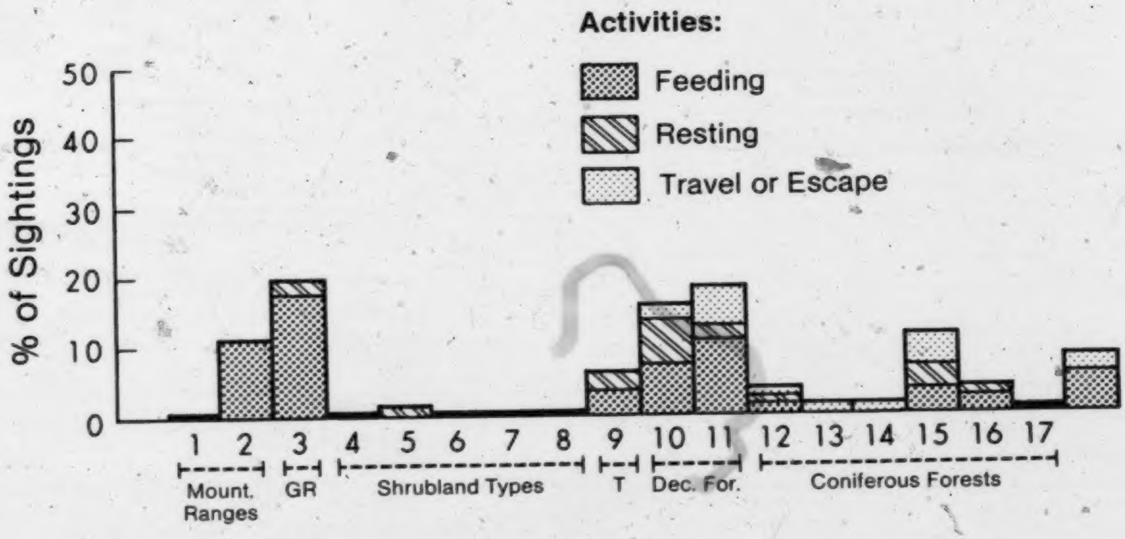

Activities:
Feeding
Resting
Travel or Escape
% of Sightings
0
10
20
30
40
50
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Mount. Ranges
GR
Shrubland Types
T
Dec. For.
Coniferous Forests

Table 3.16. Use by mule deer of major vegetation types.

MAJOR VEG. TYPE	SIGHTINGS %	ACTIVITIES F	R	T	% OF TOTAL FEEDING OBSERV.
MOUNTAIN RANGES	10.4	100	0	0	17
GRASSLANDS	19.5	83	7	0	29
SHRUBS AND THICKETS	7.8	50	50	0	6
DECIDUOUS FORESTS	32.5	56	20	20	28
CONIFEROUS FORESTS	22.1	29	36	35	11
DISTURBED (road sides, etc.)	7.9	67	0	33	8

F=Feeding
R=Resting
T=Travel or escape

grasslands ranked second with 22.1 and 19.5 percent of sightings respectively.

The use of deciduous forests was evenly distributed between the two types, Populus tremuloides-Elymus innovatus and Populus tremuloides-P. balsamifera, while observations in coniferous forests mostly occurred in the Pinus-Elymus type. Mule deer were not observed in shrubland types, but in one instance, and only occasionally in thickets (6 percent of sightings). Open mountain ranges and disturbed sites (road sides, etc.) received 10.4 and 7.9 percent of use, respectively.

The difference in the use of vegetation type are particularly relevant when considered in terms of activity patterns. Open mountain ranges and grasslands were of major importance as feeding grounds (Table 3.16), with forty-six percent of the total number of feeding observations (n=48) occurring in these two habitats, compared to 28 percent in deciduous forests. In the latter both grazing on Elymus and browsing on aspen regeneration was observed. Overall these results reflect spring feeding habits of deer described by many studies, that is a higher consumption of grasses and a decrease in browsing compared to the other seasons (see Kufeld et al., 1973 for a review).

Coniferous forests received minor use for feeding but mostly provided bedding and travel cover. Bedding activities were also recorded in deciduous forest types. However, in this regard it seems that the Populus *tremuloides*-*Elymus innovatus* type was preferred to the *Populus tremuloides*-*P. balsamifera* type (Figure 3.17). The latter is usually present in moister sites and this may account for the difference.

One of the most applied rule in deer habitat management is that a mixture of plant communities provides a better habitat than any single community (Wallmo, 1978: p. 39). The rationale behind it is based on the theory that higher habitat diversity offers more chances for a browser of finding a widely dispersed high nutritional forage (Leuthold, 1977: p. 249). The results of this study tend to support this contention since more than 70 percent of deer observations occurred in areas of high vegetational heterogeneity (Table 3.17).

Table 3.17. Distribution of mule deer on the vegetational heterogeneity gradient.

	VEGETATIONAL HETEROGENEITY					
	0	1	2	3	4	5
% OF SIGHTINGS	0	10.4	19.5	44.2	24.7	1.3

However, the selection of highly diversified habitats can be seen also as an adaptive response to the environment related to the social characteristics of the species (*e. g.*, anti-predator strategy). Further, on the Ya Ha Tinda Ranch study area, low population density and small herd sizes may have played an important role in deer distribution over the vegetational environment.

Mule deer distribution in terms of distance from forest cover in part is related to their preference of heterogeneous habitats. In fact 76 percent of observations on open country (mountain ranges and lower grasslands) occurred within 75 meters from forests, while in only two instances were mule deer observed farther than 225 meters from forests.

3.332. Physical environment

On the Ya Ha Tinda Ranch study area during the spring of 1976 mule deer were mostly found at low elevations (average 1,726 m) and on level or gently sloping ground (average 7.5 percent of slope). They were strongly associated also with smooth and grassy sites (Table 3.18). The use in spring of gentle slopes has been also reported in other studies (Mackie, 1970). Several authors, however, have underlined an apparent preference for steeper slopes (Loveless, 1964) and more rugged and higher ranges (Hudson *et al.*, 1976). This difference can be accounted for by local environmental conditions, *i. e.*, snow cover and vegetation. In this regard, Hudson *et al.* (1976) noted that selection by mule deer of rugged country may have been related more to the characteristics of the vegetation than to the degree of slope and rockiness.

Table 3.18. Use by mule deer of the physical environment measured by elevation, slope and degree of rockiness.

	ELEVATION RANGES 1,500-1,700m	 1,701-1,900m	 1,901-2,700m
% OF SIGHTINGS	55.8	44.2	0

	SLOPE RANGES 0-15%	 16-28%	 29-50%	 50%-+
% OF SIGHTINGS	75.3	16.9	7.8	0

	DEGREE OF ROCKINESS 0	 1	 2	 3	 4
% OF SIGHTINGS	88.3	11.7	0	0	0

3.333. Weather and thermal environment

The impact of winter weather on the welfare and productivity of mule deer populations has been reported in many studies (Crete, 1976 a,b; Kucera, 1976; Severinghaus, 1972). However, little is known about the relationships between meteorological factors and deer behavior in spring. In fact, the only specific study on the subject I am aware of was conducted by Loveless (1964) in northcentral Colorado. The author described daylight spring movements by mule deer towards shaded areas or into forest cover when ambient temperature reached 7° or 10°C (see also Mackie, 1970). Loveless (op. cit.) further noted that during the day the animals continually changed their position in order to remain under some shadows. However, little relation was observed between wind speed and deer behavior except during cold days with temperatures of -10°C or below.

The results of this study generally support Loveless' observations. Although no relationship was found between use of cover at sunrise and meteorological variables, significant correlations were obtained during daylight hours and in the evenings, as shown in Table 3.19.

During daylight hours mule deer were found more frequently in cover when ambient temperatures were high. Wind speed was not significantly correlated with this shelter-seeking behavior; however, when wind was entered with temperature in the windchill index, it actually reversed the direction of the relationship, indicating a

Table 3.19. Correlations between use of cover by mule deer in spring and meteorological variables at different times of the day.

	MR n=11	MD n=31	EV n=35
AMBIENT TEMP.	.14	.34*	.47**
WIND SPEED	-.18	-.23	-.55**
CLOUD COVER	-.15	.26	-.08
WINDCHILL	-.14	-.35*	-.48**

MR= Morning (dawn-1/2 hr after sunrise)
MD= Midday
EV= Evening (1/2 hr before sunset-dusk)

* = 0.01<P<0.05
**= 0.001<P<0.01

cooling effect on the animals.

Correlation coefficients between shelter-seeking behavior and meteorological variables are stronger at sunset. At this time the opposite effects of ambient temperatures and wind speed are both significant and result in a highly positive correlation between use of cover and the windchill index.

During day-light ambient temperatures reached the highest values. Therefore the weaker response to them at this time indicates the presence of other unidentified factors (e. g., intrinsic circadian rhythms) determining mule deer behavior and somewhat concealing their reaction to heat stresses. In the evenings it appeared that during warm weather grazing activities on the open grasslands and mountain ranges were delayed.

Multiple step-wise regressions were calculated for use of cover and meteorological variables. The regression obtained for use of cover at sunrise was not significant, even though ten percent of the variation was explained after the introduction of wind, temperature and cloud cover.

Regressions and summary tables for use of cover by mule deer during day-light and at sunset are shown in Table 3.20. The percent of variation in the use of forest cover during the day explained jointly by temperature, clouds and wind was 22.3 percent. The overall F test was significant at .04 when only ambient temperature and cloud cover were in the equation (19.9 percent of variation explained) but lost

Table 3.20. Multiple step-wise regression between midday use of cover by mule deer in spring and meteorological variables. Overall F test and summary table.

Use of cover during the day = -.81 +.012 T +.002 C -.013 W

Multiple R = .472
R square = .223
Adjusted Rsq = .136
Standard error = .279

Analysis of Variance	DF	SS	MS	F
Regression	3	.603	.201	2.578
Residual	27	2.11	.078	n.s. at P<.07

Summary table:	Multiple R	R square	Rsq change
Ambient temp. (T)	.345	.119	.119*
Cloud cover (C)	.446	.199	.080
Wind speed (W)	.471	.223	.023

* 0.01<P<0.05

.../continued

Table 3.20 continued...

```
==========================================================================
==========================================================================
    Use of cover at sunset = -1.76 -.081 W +.037 T +.004 C
==========================================================================
==========================================================================

    Multiple R       = .69     Analysis of Variance  DF     SS      MS     F
    R square         = .48        Regression          3   4.17    1.39   9.55***
    Adjusted Rsq     = .43        Residual           31   4.51    0.14
    Standard error =.38

--------------------------------------------------------------------------

    Summary table:               Multiple R          R square            Rsq change
      Wind speed (W)               .555               .308                .308***
      Ambient temp.  (T)           .627               .393                .085*
      Cloud cover (C)              .693               .480                .087*

--------------------------------------------------------------------------

*    0.01<P<0.05
***  0.0001<P<0.001
```

statistical significance after the introduction of wind speed. Yet in terms of individual contribution only ambient temperature was significant, while the improvement brought in by cloud cover and wind speed (8 and 2.3 percent respectively) could be the result of chance.

With regard to the use of cover at sunset the linear combination of wind speed, ambient temperature and cloud cover accounted for a highly significant 48 percent of the variance. Thirty percent was first explained by wind speed. After its introduction into the equation ambient temperature and cloud cover accounted for 8.5 and 8.7 percent of variation respectively. The regression equation indicates that the use of cover by mule deer in the evenings decreased with increasing wind speed and increased with increasing air temperature and cloud cover.

The relationship between cloud cover and shelter-seeking behavior is difficult to interpret when considered in isolation (simple correlation coefficient=.08; n.s.). The significant contribution to the regression may reflect local microclimatic conditions undetected in this study.

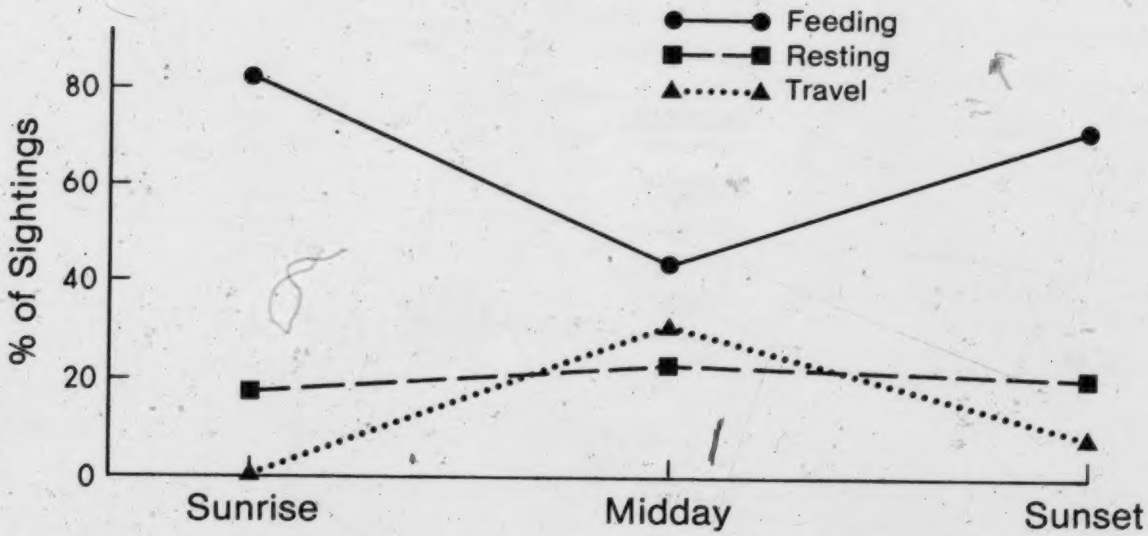
Multiple step-wise regressions were calculated also by replacing wind speed and ambient temperature with the windchill index. Markedly less variance was explained, since the values obtained at different times of day were 4.3, 7.9 and 26.6 percent respectively.

3.334. Daily patterns of activity

The daily activity patterns of mule deer observed in this study are well known in the literature (Mackie, 1970). Figure 3.18 shows the percentage of all mule deer observed in different activities at sunrise, during the day and at sunset. Feeding was the predominant activity observed throughout the study. However, a significant decrease was observed during daylight hours ($t=\pm2.265$; $P<0.05$) and again an increase at sunset ($t=\pm2.165$; $P<0.05$). Loveless (1964) suggested that in spring much of the feeding activity occurred at night as a response to the thermal environment. With rising ambient temperature mule deer sought shade in forests and bedded down. Although in this study the animals' response to ambient temperature was documented (section 3.333), a marked increase in bedding activity was not observed. This may reflect different environmental conditions. That is, availability of forage and browse in deciduous forests in the study area offered a substitute feeding to the preferred grasses in open grasslands and mountain slopes.

The marked increase in travel activities during daylight hours can be explained largely by movements to and from the open country.

Figure 3.18. Percentage of all mule deer observed in different activities at different times of day.


Feeding
Resting
Travel
% of Sightings
80
60
40
20
0
Sunrise
Midday
Sunset

CHAPTER FOUR

RESOURCE PARTITIONING

4.1. Introduction

Field studies on the ecology of grazing animals have been concerned mostly with descriptions of range conditions, food habits and habitat requirements. However, because of the profound impact that niche and competition theories have had on the development of wildlife science in North America, the assessment of interspecific interactions has been limited substantially to empirical determinations of food and space overlaps (Julander, 1958) and such overlaps have been regarded as measures of competition.

In the 1950's and 1960's a descriptive approach was frequently followed and the degree of competition occasionally was determined on the basis of whether the coexisting ungulates were mostly grazers or browsers (e. g., Cowan, 1947). In numerous studies descriptive comparison of the amounts and species of plants eaten and/or habitat use were presented (Stevens, 1966; Constan, 1972).

More recently, in an attempt to quantify the presence of species in the environment, a variety of indices of interspecific association and resource overlap, directly derived from theoretical ecology (Dice, 1945; Cole, 1949;

Horn, 1966; Levins, 1968), have been adopted. Such indices have been widely used for determining competitive relationships between North-American ungulates (Telfer, 1972; Compton, 1974; Irwin, 1975; Anthony and Smith, 1977). In fact, spatial and forage overlaps between two or more ungulates usually are interpreted as a sign of actual or potential competition.

Several authors have recognized the limitations of this approach that implicitly asserts that interactions can only be negative (Hudson *et al.*, 1974). Schoener (1974) remarked that ecologists "...in order to make a case for the importance of competition in nature...in exchange for a direct demonstration of ongoing competition, attempt to implicate competition indirectly".

With regard to the use of indices of overlap, Colwell and Futuyma (1971) pointed out that "...overlap in resource use by two species in nature can be evidence either for or against the existence of competition between them". This concept was later emphasized by Sale (1974). In his words "...when several species coexist, the amount by which they overlap in their use of resources is a measure of their similarity to one another. As such, resource overlap does not measure the amount of competition among them" (p. 245). Sale, recognizing the usefulness of indices of overlap, regretfully notes the unfortunate and mistaken assumption, made by many authors, of "...a direct correlation between degree of overlap and intensity of competition..." (Sale, 1974: pp. 245-246).

The inadequacy of this approach is further underlined by a series of studies conducted in East Africa and Europe. In East Africa up to twenty ungulate species may coexist in limited areas at a time when the food resources are critically low (Lamprey, 1963). The existence of grazing successions among East African ungulates and the dependence of one grazing species on the previous grazing of others, was first suggested by Vesey-FitzGerald in 1960 and subsequently described by Gwynne and Bell in 1968. Further details on the facilitative interactions among East African ungulates, in spite of spatial and forage overlap, were later given by Bell (1971) and McNaughton (1976). The latter author in particular, after having studied interactions between wildebeest (Connochaetes taurinus albojubatus) and Thomson's gazelle (Gazella thomsoni), noted that grazing by wildebeest facilitates "...total nutrient and energy flow to the gazelle population..(by)..converting a senescent plant community into a productive one..(and)....improving forage quality" (McNaughton, 1976: p. 94).

It has been suggested that the complex and subtle interactions observed in wildlife communities, and between them and their environment, in tropical ecosystems are the result of longer evolutionary history (Hudson, 1976). However, there are indications that similar interactions may exist in temperate zones and that, by considering wild ungulates apart from the environment where they evolved in, field evidence can be easily missed or misinterpreted. In this respect noteworthy is Batcheler's study (1968) on roe deer (Capreolus capreolus), fallow deer (Dama dama) and red deer (Cervus elaphus) association with different forest successions in England.

With regard to the North-American continent, Hudson et al. (1974) noted that bighorn sheep grazing occurred on regrowth areas where ever possible and that such areas were found on sites stressed either by grazing and trampling or by edaphic factors. This behavior was related to the species preference of high quality forage (Hudson et al., 1974), i. e., it is known that grazed plants are of higher nutrient value than ungrazed ones (Jameson, 1963). These observations suggest the possibility of facilititive interactions between a non-selective and a selective grazer, e. g., wapiti and bighorn sheep respectively, in the form of an improvement in forage quality. Although there is no experimental evidence yet that this actually occurs in natural ecosystems in temperate areas, a similar improvement in winter forage quality for elk was in fact achieved by Anderson and Scherzinger (1975) using livestock grazing in late spring and early summer (see also Mackie, 1970:p. 73, for cattle and deer).

Positive interactions between species have received little attention in ecology (Odum, 1971). Therefore it is difficult to apply the concepts of protocooperation or commensalism to the facilitative interactions observed between ungulate species.

With regard to negative interactions, according to the theory two forms of competition can be distinguished: exploitation and interference (Miller, 1967). The first is the result of the "free access" by the 'competing' species to the same resource, with "little or no spatial interaction" between them (Miller, 1967). Interference instead applies to cases when one individual or species limit the access of the others to a 'required' resource. Telfer (1974 in Cairns, 1976) noted that interactions among North American game mammals are more exploitative than interfering. However, the correct interpretation of Gause's competition law requires resources to be limited (Darlington, 1972; Sale, 1974). There is no evidence that such is the case in mixed grazing systems unless human activities have altered the distribution of large populations of ungulates, by compressing them in restricted areas or by limiting their access to otherwise available habitats, or have modified their natural environment. In these situations resources will be limited regardless of whether there are two or more ungulate species or just one. The ecological concept of competition does not seem to apply in such cases but the biologist would be dealing with a problem common in management of domestic grazing systems, that is assessing carrying capacity of the range and defining stocking rates. On the other hand, because it is believed that competitive interactions have played an important role in the evolution of species diversity (Dobzhansky et al., 1977: pp. 249, 341), the present coexistence of several similar species would suggest that they may have evolved species-specific mechanisms such as character displacement (Brown and Wilson, 1956) to minimize competition (see Wilkinson et al., 1976: p. 161).

There are many dimensions along which species-specificity may have developed. Schoener (1974) reviewing studies on resource partitioning in ecological communities pointed out that in 55 percent of cases ecological separation among coexisting species was mainly achieved on the basis of habitat structure, while in 40 and 5 percent of studies food preference and time of use played a more important role respectively. With direct regard to coexisting ungulate species the importance of habitat factors (Ferrar and Walker, 1974; Hudson et al., 1976; Stocker et al., 1977) and forage selection (Vesey-FitzGerald, 1965) has been emphasized. Several studies (Gwynne and Bell,1968; McNauhton, 1976; Batcheler, 1968; Hudson et al., 1974) have suggested separation among herbivorous species along a forage quality gradient. It seems however more likely that the successful coexistence of ungulates in mixed grazing systems is made possible by their ecological separation along several dimensions whose complementarity and synergism can vary in different environments (Lamprey, 1963; Hirst, 1975; Hudson, 1976). In addition, it should be emphasized that the coexistence of similar species in any ecosystem is a dynamic process in which population densities and environmental feedbacks play important roles. Therefore, results of an investigation should not be considered as stable ecological relationships among the coexisting species (Hudson, 1976).

4.2. Approach

When this project was initiated the possibility of adopting recent new approaches to the study of natural grazing systems was considered. Developments in niche theory (Hutchinson, 1957), and the application of multivariate analysis for describing niche patterns (Green, 1971; Shugart and Patten, 1972; Ferrar and Walker, 1974; Hudson, 1976), seemed to offer a promising tool for understanding and resolving species interactions, consequences of habitat changes, and other practical problems which are met daily in wildlife management. However, a review of literature on niche theory and resource partitioning among ungulates indicates several limitations. In fact it seems that on a theoretical level, controversy still surrounds the meaning and importance of the words niche and competition (Darlington, 1972; Krebs, 1972; Whittaker et al., 1973; 1975). Further, the niche theory and indices of ecological overlap, possibly of great significance in population ecology, seem inadequate to fully explain and represent the complex set of functional interactions that may exist in a mixed grazing system. For these reasons, the study of resource partitioning among bighorn sheep, elk and mule deer on winter ranges on the Ya Ha Tinda Ranch study area was limited to a descriptive comparison of their habitat preferences. No attempt was made to quantify interspecific interactions. Even though a descriptive investigation of the equilibrium state of a process often reveals little about what that process is (Hudson, 1976), it is believed such an investigation can be regarded as the first step after which that understanding can be achieved.

4.3. Methods

Resource partitioning among bighorn sheep, elk and mule deer was inferred by comparing their occupational patterns and spatial distribution described in Chapter 3.

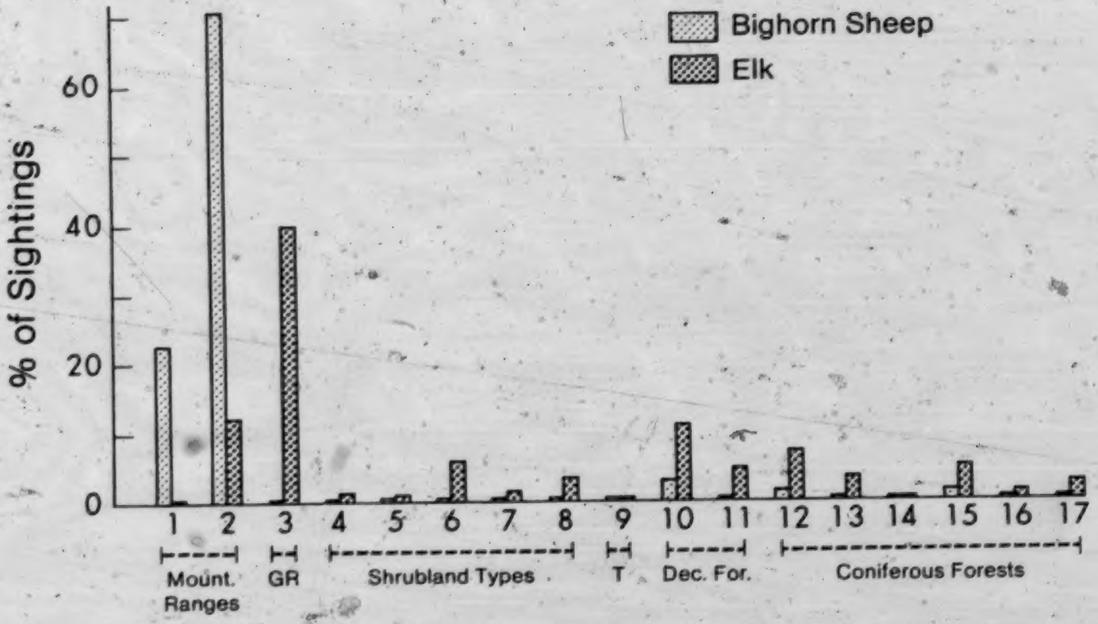
4.4. Results and Discussion

4.41. Winter (Elk-Bighorn sheep relationships)

Occupational patterns and distribution of elk and bighorn sheep indicate two well defined winter ranges.

The use of vegetation types is compared in Figure 4.1. Bighorn sheep were mostly found on open mountain ranges. The occasional use of forest types was associated

Figure 4.1. Distribution of bighorn sheep and elk sightings by vegetation types in winter.


Bighorn Sheep
Elk
% of Sightings
0
20
40
60
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Mount. Ranges
GR
Shrubland Types
T
Dec. For.
Coniferous Forests

with movements to and from salt licks. In contrast elk were mostly observed on the valley floor, in the open grasslands and in the surrounding forests. The use of low elevation mountain ranges was minor and it was related to their 'strategic' location in the study area. In fact, this habitat was largely used as an escape route during the January and February special hunting season as previously described (see sections 3.321 and 3.325). The small overlap between elk and bighorn sheep therefore does not represent a stable natural condition. However, it can be speculated that any greater displacement of the elk population from the main grassland could result in increased use of the lower mountain ranges and, hence, in increased possibilities of interactions, positive or negative, between the two species.

In terms of vegetational heterogeneity, bighorn sheep were generally found in less diversified habitats than elk (Table 4.1).

Table 4.1. Winter distribution of bighorn sheep and elk on the vegetational heterogeneity gradient. (Percent of sightings).

	VEGETATIONAL HETEROGENEITY					
	0	1	2	3	4	5
BIGHORN SHEEP	0	53.5	35.2	11.3	0	0
ELK	3.4	18.4	39.1	25.3	8.0	5.7

Vegetational heterogeneity: number of vegetation types within 250 m radius.

Ecological separation in winter between bighorn sheep and elk is further indicated by their distribution in the physical environment. Figure 4.2 graphically shows the relative positions of the two species on three descriptors, elevation, percent of slope and degree of rockiness. Bighorn sheep are found on high elevation, steep, rugged country, whereas elk prefer lower elevation and less steep, grassy ranges.

During the winter months the two species were never jointly observed. Their distinct spatial distribution mostly prevented any behavioral interaction. Occurrences of bighorn sheep on the valley floor were restricted to the use of salt licks along the banks of Scalp Creek (Figure 1.1). Because of the steepness of their location (80°) elk did not have access to them.

4.42. Spring (Elk-Bighorn sheep-Mule deer relationships)

The relative use of vegetation types by bighorn sheep, elk and mule deer during spring of 1976 is shown in Figure 4.3. In this season bighorn sheep and elk continued to be largely distinct in their use of vegetation types, but mule deer to a certain degree overlapped with both species. Specifically mule deer were observed grazing on open mountain ranges and on grasslands, major habitats for bighorn sheep and elk respectively, and used forest types where both the other species frequently occurred. Overlap

Figure 4.2. Winter distribution of bighorn sheep and elk in the physical environment.

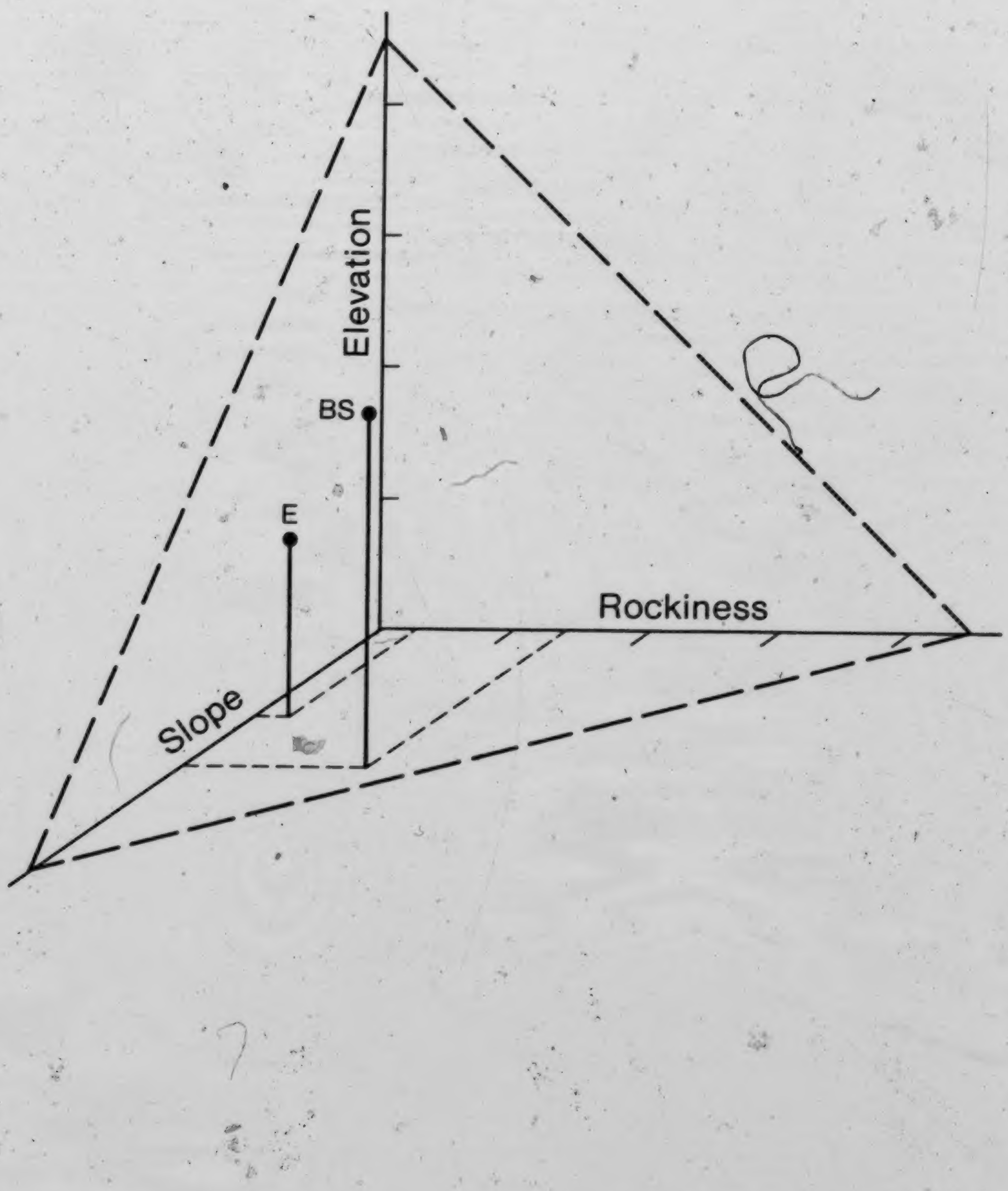
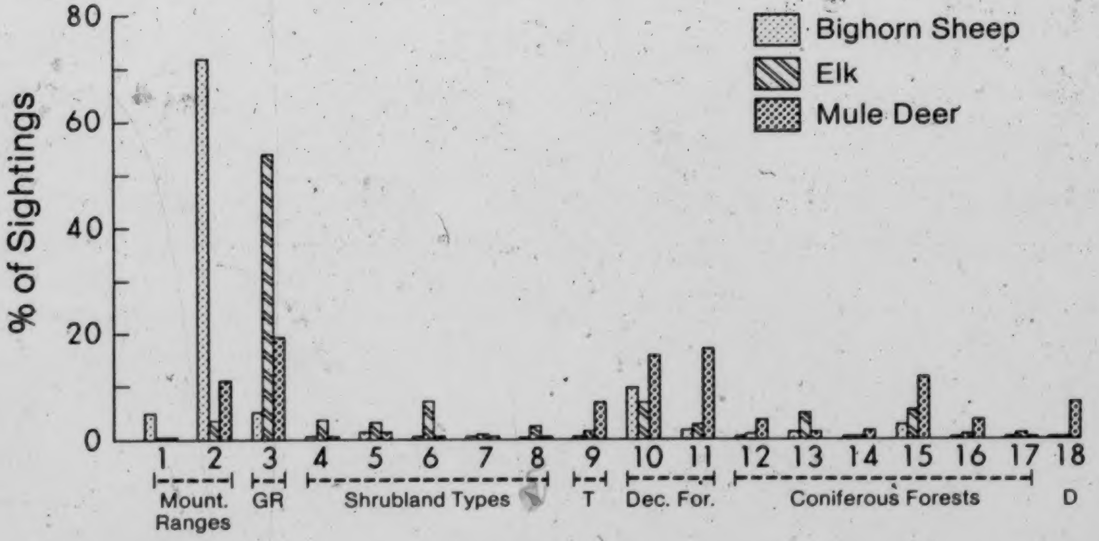

Elevation
BS
E
Rockiness
Slope

Figure 4.3. Distribution of bighorn sheep, elk and mule deer sightings by vegetation types in spring.


80
60
40
20
0
% of Sightings
Bighorn Sheep
Elk
Mule Deer
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Mount. Ranges
GR
Shrubland Types
T
Dec. For.
Coniferous Forests
D

among the three species is evident in the use of deciduous forests, the Populus tremuloides-Elymus innovatus type in particular, where mule deer, bighorn sheep and to a lesser extent elk were observed with similar frequency. Such overlap may be a reason for concern if the size of the wildlife populations is taken into account. For instance the behavioral desplacement of a small herd of mule deer by a herd of 100-200 elk could be suggested[1]. However, it should be pointed out that overlap in the use of a vegetation type does not imply spatial overlap. A vegetation type is identified by the composition and structure of the vegetation. Its location relative to other communities was not a factor considered. Yet the importance of a vegetation type for an ungulate species varies not only on the basis of physiographic or vegetational characteristics of the site, but also of its proximity to other communities that provide preferred feeding ground or bedding cover. In this study elk and mule deer used deciduous forests which are different even though they were classified as the same vegetation type. Elk were associated with the Populus tremuloides-Elymus innovatus type located in proximity of the open grassland (largely in the eastern section of the study area), whereas the Populus tremuloides-Elymus innovatus type used by mule deer consisted of patches in coniferous forests and at the bottom of mountain slopes. The use of coniferous forests differed in a similar way. The _Pinus contorta_-_Shepherdia canadensis_ type provided elk with important bedding cover near their preferred feeding ground, the main grassland on the valley floor, while mule deer used it in highly heterogeneous areas, when interspersed with deciduous forests and patches of grassland.

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[1] NOTE: In this study any sighting is regarded as one observation regardless of herd size.

Use of the main grassland by elk and mule deer followed the same pattern. Elk were observed mostly on level ground in open country at darkness while mule deer were observed throughout the day on broken areas near thickets and patches of shrubs.

Overlap in the use of deciduous forests and open mountain ranges between bighorn sheep and mule deer partly reflects spatial overlap between the two species. However, the use of deciduous forest by bighorn sheep should be considered occasional as it was mostly related to their responses to the thermal environment (section 3.511c).

Behavioral differences between elk, bighorn sheep and mule deer in their use of vegetation types were further indicated by the degree of vegetational heterogeneity they preferred (Table 4.2). Bighorn sheep were mostly found in habitats of low heterogeneity while mule deer were found in areas with high vegetational heterogeneity. Elk appeared to occupy an intermediate position.

Table 4.2. Bighorn sheep, elk and mule deer distribution on the vegetational heterogeneity gradient. (Percent of sightings).

	VEGETATIONAL HETEROGENEITY					
	0	1	2	3	4	5
BIGHORN SHEEP	1.3	27.5	46.3	20.0	5.0	0
ELK	4.7	22.0	36.7	25.3	10.0	1.3
MULE DEER	0.0	10.4	19.5	44.2	24.7	1.3

Vegetational heterogeneity: no. of vegetation types within 250 m radius.

The distribution of the three ungulates in the physical environment is shown on Figure 4.4. Bighorn sheep are definitely separated from the two cervid species on the basis of elevation, percent of slope and degree of rockiness. Elk and mule deer were similar in their preference of rolling and grassy ranges. However, they were separated on the elevation gradient.

The use of vegetation types by bighorn sheep, elk and mule deer and their distribution in the physical environment reflect the spatial separation that was in fact observed in the field (Figure 4.5). Elk ranged on the valley floor, bighorn sheep on the surrounding mountain slopes, while mule deer mostly occupied an intermediate area. Overlaps occurred between mule deer and bighorn sheep and between mule deer and elk.

The data collected in this study also indicate little spatial interference among the coexisting species. In Table 4.3 joint observations are tabulated and described. Interspecific aggressive behavior was never observed. Instead, each species seemed indifferent to the presence of the other. These observations, although limited in number, concur with Kramer (1973) who noted interference between deer and other ungulates to be "unimportant" at distances over 50 meters. Yet in the only instance where mule deer and bighorn sheep were jointly observed the two species intermingled and no reaction was observed (Figure 4.6).

Figure 4.4. Spring distribution of bighorn sheep, elk and mule deer in the physical environment

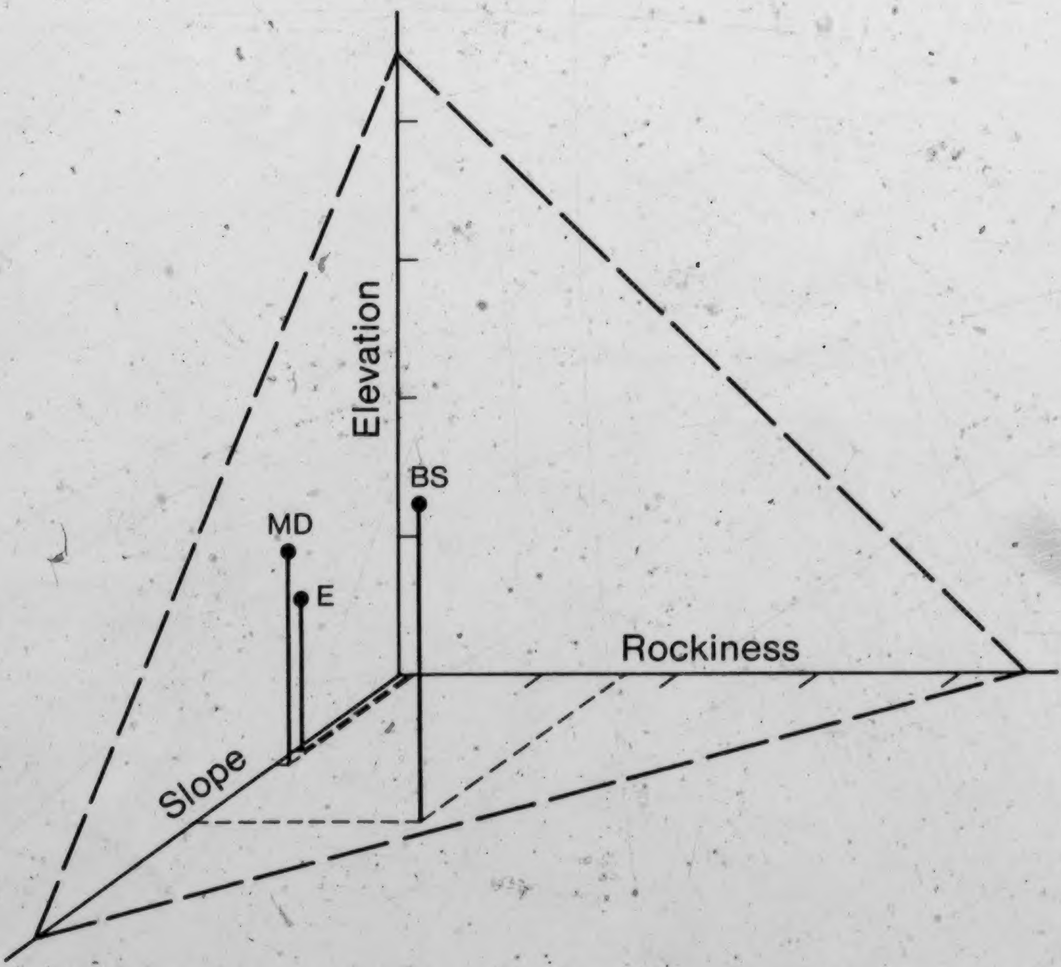
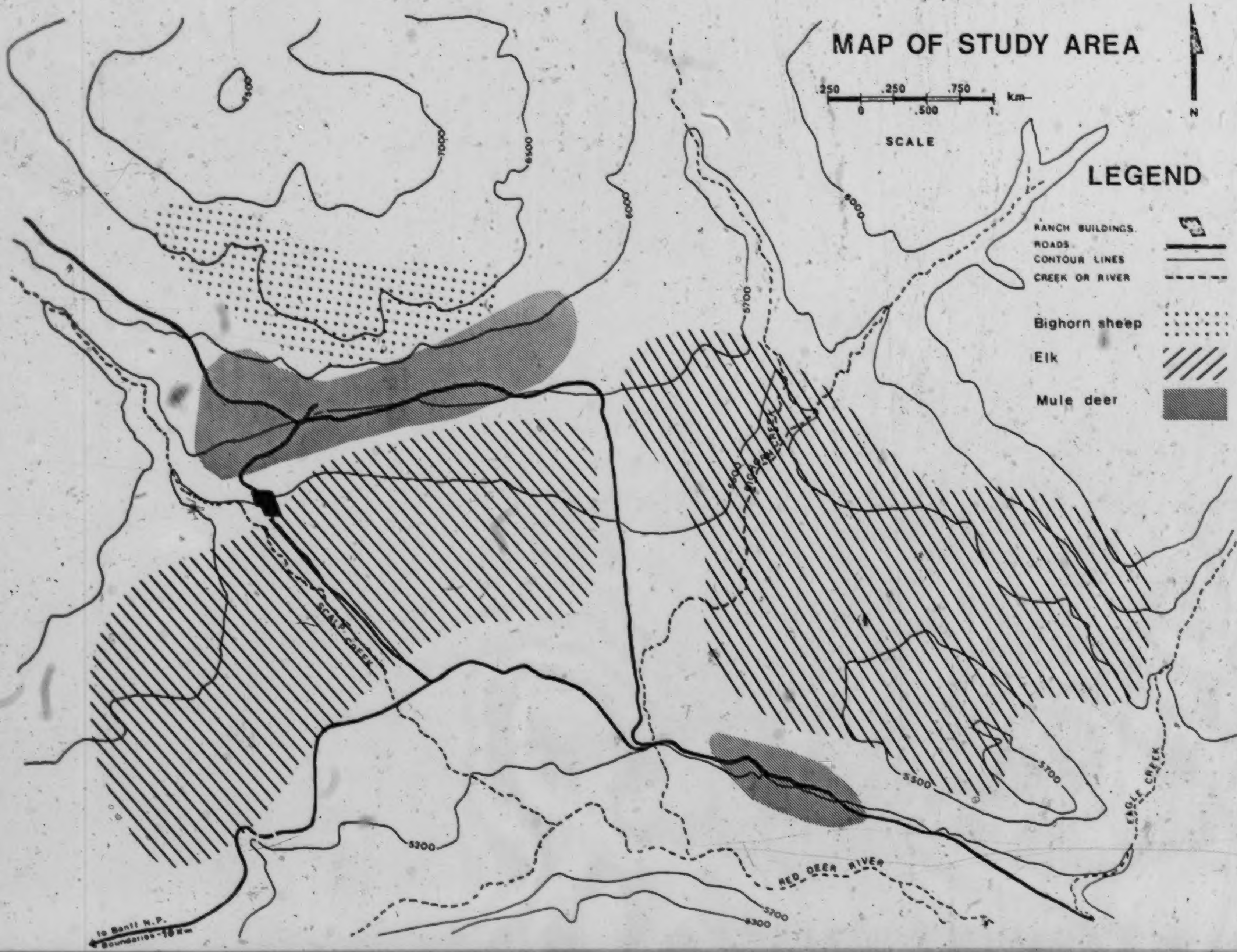

Elevation
BS
MD
E
Rockiness
Slope

Figure 4.5. Spatial distribution of bighorn sheep, elk and mule deer on the study area in spring.



MAP OF STUDY AREA

.250
0
.250
.500
.750
1.
km
SCALE
N
LEGEND
RANCH BUILDINGS.
ROADS.
CONTOUR LINES
CREEK OR RIVER
Bighorn sheep
Elk
Mule deer
7500
7000
6500
6000
6000
5700
5500
5700
5500
5200
5200
5300
BIGHORN CREEK
SCALP CREEK
EAGLE CREEK
RED DEER RIVER
To Banff N.P.
Boundaries - 18 Km

Table 4.3. Joint observations of wild ungulates and horses on the Ya Ha Tinda Ranch study area from December 1975 till May 1976.

	Bighorn sheep	Elk	Mule deer	Horses
Bighorn sheep	-			
Elk	3*	-		
Mule deer	1**	2***	-	
Horses	2****	6****	0	-

* April 13: 1 bull elk, 3 bighorn sheep rams grazing on open mountain slope, within 100 meters from each other.

April 19: 3 elk cows, 8 bighorn sheep ewes and yearlings, 3 rams grazing on open mountain slope, within 50 meters from each other.

May 15: 1 elk bull, 13 bighorn sheep rams grazing on mountain slope within 150 meters from each other.

** May 17: 3 mule deer, 18 bighorn sheep ewes and yearlings grazing together in deciduous forest (_Populus tremuloides_-_Elymus innovatus_ type).

*** May 15: 1 elk bull, 3 mule deer does and 1 yearling grazing on open mountain slopes within 50 meters from each other.

May 16: same as the previous day.

**** See text.

Figure 4.6. Joint observation of mule deer and bighorn sheep in a deciduous forest.

During the study white-tailed deer were observed only on four occasions. For this reason the distribution of the species could not be considered in quantitative terms. However, it is interesting to note that in three of the four observations white-tailed deer were intermingled with mule deer (Figure 4.7 a and b). A review of interspecific behavior between these two deer species can be found in Kramer (1973).

4.43. Horses and wild ungulates

In the present study an assessment of the impact of domestic horses on wildlife populations was sought from direct observations of animal behavior. A detailed analysis of distribution and habitat selection of horses could not be carried out because their use of the available environment was found to be largely affected by management practices. Horses ranged widely throughout the open range on the valley floor, their distribution and herd size determined by the location of fences, artificial salt licks and, in the case of two herds, by morning supplemental feeding. Further, occasionally some herds were rounded up and counted or moved to another area.

Horses were found mostly on the grassland and therefore their range overlapped with that of the elk population. Yet some spatial separation between the two species was observed and was related to the differential

Figure 4.7 a,b. Joint occurrence of mule deer and
white-tailed deer.

a.

b.

reaction to human activities. Use of the grassland by elk was restricted to areas close to forest glades (see sections 3.1512 d and e) while horses could be found throughout the day in the middle of the main grassland. However, this separation was possibly limited to daylight since at night elk would move farther from cover and make use of the available range.

Diet overlaps between feral horses and elk have been recently reviewed by Salter (1978). The author reported in his study area, located only 30 km east of the Ya Ha Tinda Ranch, overlaps of 51 percent in winter and 28 percent in spring. No data is available for the Ya Ha Tinda Ranch. However, McGillis (1977) noted that, based on forage production, the ranch could support a doubled number of horses (409) and elk (852)[1]. Even if the author did not consider the many factors that may affect the distribution of the two species and cause overgrazed conditions in sections of the ranch, his figures and the relatively small diet overlap reported by Salter (1978) suggest little negative interactions between elk and horses in the study area.

With regard to behavioral interactions between the two species, no spatial interference was ever observed. In the six instances horses and elk were jointly observed, the animals were intermingled, feeding together. The distance between individuals of the two species was not more than a few meters. On one occasion a playfull herd of 20 horses, running at dusk on the open grassland, spooked an extremely wary elk herd that was just coming out of cover. However, the elk's reaction lasted only a few minutes and the animals returned to their previous activity.

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[1] NOTE: The highest number of elk ever recorded grazing at any time on the Ya Ha Tinda Ranch from 1975 to 1978 was some 400 individuals (personal observations).

Spatial overlap between horses and mule deer or bighorn sheep was negligible and non-existent respectively. However, in several instances a small herd of bighorn sheep was observed using blocks of salt lick located in the ranch houses' backyard. Here in two cases they were observed jointly with a small number of young horses. In one instance horses approaching bighorn sheep caused them to move away.

CHAPTER FIVE

CONCLUSIONS AND MANAGEMENT CONSIDERATIONS

In this study, by using a descriptive approach, a definite pattern of resource partitioning among bighorn sheep, elk and mule deer on the Ya Ha Tinda Ranch area was found. Ecological separation was achieved on a combination of vegetational and physiographic parameters and was reflected by the species-specific spatial distribution.

The analysis of habitat selection and spatial distribution of each individual species revealed several factors which may determine or alter habitat use and resource partitioning. Among them, the behavioral response of the elk population to human disturbance was probably the most important. Harassment during the special hunting season in fact forced the elk to avoid their prime winter range and to spatially overlap with bighorn sheep. In addition their extreme wariness appeared to cause a sub-optimal use of the environment whose consequences in terms of population productivity are not known.

The thermal environment was also found to affect resource partitioning. Use of deciduous forest by bighorn sheep for instance and their consequent overlap with mule deer in spring, was largely interpreted as a response to heat stress.

These results indicate that ecological relationships among coexisting ungulates and between them and their environment are not fixed in time and space, but are of a dynamic nature. Therefore, the pattern of resource partitioning described in the present study may be different in other locations and/or with other environmental conditions.

Within this context management of a wild ungulate community has to be time and site specific, based upon the knowledge of each component species, its use of the environment and the factors that may alter it. On the Ya Ha Tinda Ranch, during the winter and spring of 1975-76, bighorn sheep, elk and mule deer were found separated in their distribution and use of the vegetation. This may reflect the low population levels and generally mild microclimatic conditions. For instance, it can be speculated that an unusual winter with heavy snow falls may force elk to vacate the main grassland on the valley floor and to shift to browsing habits, hence potentially interacting with mule deer, or to move to higher elevations on wind-blown mountain slopes, hence potentially interacting with bighorn sheep.

The results of this study indicate that displacement of elk from the main grassland due to hunting or human activities may lead to habitat overlap with bighorn sheep. In this regard management definitely should strive to limit disturbance of the elk population.

In this study little emphasis has been given to the food habits of the three ungulates. However, it is believed that food habits were indirectly reflected by the use of vegetation types. Browse and grass species in all vegetation types appeared in good condition, even though several years before willow species (Salix glauca and Salix spp.) appeared to have been severely browsed by elk.

The elk population is the largest ungulate population in the study area and therefore the concomitant use with horses of the main grassland has received much attention during the last twenty years. Several reports have been submitted (Flook, 1957; Webb, 1961; Neave, 1970; McGillis, 1977) dealing with range conditions and number of elk wintering on the main grassland. The range has been reported as being heavily overgrazed and rough fescue (Festuca scabrella), the most dominant grass species and a plant sensitive to heavy grazing, no longer present (C. Hayes in Neave, 1970). However, these conclusions were not borne out by recent studies. McGillis (1977) summarizing forage production studies conducted on the Ya Ha Tinda Ranch during 1962-63 and 1973-74 reported the continuing presence of rough fescue and the range in good condition (also pers. obs.). With regard to the size of the elk population this is reported to have ranged from 150 to 1,800 individuals. That some of these figures were overestimated has been noted by Webb (1961). The author further underlined his difficulties in explaining the high number of 1,200 elk observed for a short period in 1961.

Management of the wildlife community on the Ya Ha Tinda Ranch has centered on the management of the elk population in response to presumed overgrazing. But success has been hampered by a poor understanding of its ecology, behavior and movements. Correct management of the elk herd should take into account not only range use and seasonal migrations into Banff National Park but also the factors which may affect it. In order to provide this information a comprehensive study of the elk population is being conducted by the author.

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